Stable light isotopes in fauna as environmental proxies in the Southern African winter and year-round rainfall zones

JULIE LUYT

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DECLARATION

This thesis reports the results of the original research I conducted under the auspices of the Department of Archaeology in the Faculty of Science at the University of Cape Town, between 2013 and 2016. All the assistance that I received has been acknowledged. This work has not been submitted for a degree at any other university.

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ABSTRACT

This study explores the effects of environmental and climatic variables on the stable carbon, nitrogen and oxygen isotopic values of wild African fauna from C_3 dominated environments. Most previous studies of isotopic ecology in Africa have been carried out in summer rainfall regions. This study focuses on the winter rainfall zone in the southwestern part of Africa, where important archaeological sites record evidence of early modern humans. This study focuses on contemporary fauna to provide a baseline for the interpretation of stable isotope analyses of archaeological and fossil animals from this region, a key tool in the reconstruction of palaeoclimates and palaeoenvironments. It also contributes to a better understanding of isotope systematics in large mammals.

$\delta^{13}C$ and $\delta^{15}N$ were measured in bone collagen, and $\delta^{13}C$ and $\delta^{18}O$ were measured in tooth enamel. Samples were taken from 27 species of indigenous wild mammals in game parks and nature reserves, i.e. relatively undisturbed natural environments. Animal species include primates, ungulates and carnivores collected from the following vegetation types: Savanna, Succulent Karoo, Nama Karoo, Fynbos, Afromontane Forest and Albany Thicket. Correlations between the isotopic measurements and meteorological factors were explored to assess the nature and strength of the relationships. Meteorological factors included mean annual precipitation (MAP), mean annual temperature (MAT), mean annual soil moisture stress (MASMS), mean annual potential evapotranspiration (MAPE), relative humidity (RH), summer aridity index (SAI), winter concentration of rainfall (WCR), moisture index (MI) and water deficit (WD).

The $\delta^{13}C$ values of browsers varied according to vegetation type and meteorological factors. Browsers appeared to be more sensitive environmental proxies than previously recognised, and in this region, their $\delta^{13}C$ values tracked environmental and climatic conditions more closely than grazers. Based on the sample of animals available for this study, grazers displayed selective feeding behaviours that made it difficult to interpret their $\delta^{13}C$ values. Regression models showed that $\delta^{13}C_{enamel}$ in ungulates was strongly correlated with MAT (r^2 = 0.75), SAI (r^2 = 0.75) and WCR (r^2 = 0.74). $\delta^{13}C_{collagen}$ in ungulates was most strongly correlated with MAT (r^2 = 0.60), MASMS (r^2 = 0.52), SAI (r^2 = 0.63) and WCR (r^2 = 0.65). $\delta^{18}O_{enamel}$ in ungulates showed a significant relationship with all meteorological factors except SAI. The strongest relationships were with MAP (r^2 = 0.60), MAPE (r^2 =0.63), WD (r^2 = 0.64) and MI (r^2 = 0.61). The data show that $\delta^{15}N_{collagen}$ patterning is complex. $\delta^{15}N_{collagen}$ in ungulates showed a significant relationship with five out of nine meteorological factors (MAP, MAPE, WCR, WD and MI) but the r^2 values were much lower ($\leq$ 0.32).

Regression models for carnivores showed significant correlations between both $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$ and all nine meteorological factors tested with MASM being the strongest correlation ($\delta^{13}C_{enamel}$ $r^2 = 0.67$ and $\delta^{13}C_{collagen}$ $r^2 = 0.66$). Carnivore $\delta^{18}O$ showed significant correlations with MAP, MAPE, SAI, WD and MI but as with $\delta^{13}C$, the r^2 values were low indicating that meteorological factors are not a good predictor of their $\delta^{18}O$. Carnivore $\delta^{15}N_{collagen}$ had significant correlations with the highest r^2 values, for eight out of nine of the meteorological factors; only SAI was not significantly correlated. This indicates that carnivores are likely to be effective integrators of environmental influences on animal $\delta^{15}N$. Primate $\delta^{13}C_{enamel}$, $\delta^{13}C_{collagen}$, $\delta^{18}O$ and $\delta^{15}N_{collagen}$ do not appear to have strong relationships with meteorological factors, presumably because primates change their diets to suit the environment in which they find themselves.

Multivariate models that incorporated multiple environmental variables did not significantly strengthen the correlations with the isotope values. The best understanding of the dataset therefore comes from the exploration of relatively simple analyses using seasonality of rainfall variables (such as SAI, WCR) or indices that combine two meteorological variables (like MI).

In contrast to several previous studies, enamel from different teeth along the tooth row did not show systematic patterning in $\delta^{13}C$ or $\delta^{18}O$. Median $\Delta_{enamel\text{-}collagen}$ (i.e. the difference between $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$ of the same animal) was found to be largest for ungulates at 7.1. For omnivores it was 5.5 and for carnivores it was 5.0. The median $\Delta_{enamel\text{-}collagen}$ value for ruminants was 7.2 while for non-ruminants it was 6. This is probably because ruminants produce more methane (which is depleted in ^{13}C) during digestion than non-ruminants, leaving collagen in ruminants enriched in ^{13}C. $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$ were more strongly correlated for ruminants compared with non-ruminants and for large animals compared with smaller ones. This finding makes an important contribution to our understanding of carbon isotope metabolism in animals, providing the first clear evidence from a field study that gut physiology does indeed affect $\Delta_{enamel\text{-}collagen}$ spacing

This work documents the natural variation in stable C, N and O isotopes in animals from C_3 winter rainfall biomes of Southern Africa. This provides a baseline for identifying environmental and climatic shifts in the past. By comparing isotopic analyses of archaeological fauna with contemporary fauna, the palaeoenvironmental context for the emergence of modern humans in this region can be elucidated.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

LIST OF ABBREVIATIONS

Mean annual precipitation (MAP)

Mean annual temperature (MAT)

Mean annual soil moisture stress (MASMS)

Mean annual potential evapotranspiration (MAPE)

Relative humidity (RH)

Summer aridity index (SAI)

Winter concentration of rainfall (WCR)

Moisture index (MI)

Water deficit (WD)

Evaporation sensitive (ES)

Evaporation insensitive (EI)

Water dependent (WD)

Water independent (WI)

Chapter 1: Introduction

1.1 Introduction

This thesis explores the effects of environmental and climatic variables on the stable carbon, nitrogen and oxygen isotopic ratios of bone and tooth enamel of wild African mammals from C_3 dominated environments.

This study of stable isotope patterning in modern fauna was motivated by the need for a well-characterised baseline against which to compare stable isotope analyses of archaeological and fossil animals from C_3 dominated environments. The isotopes analysed here are those most frequently used in ecological and palaeoecological studies. Previous studies of isotopic ecology in Africa have focussed primarily on summer rainfall regions. In contrast, the present study highlights the winter rainfall zone in the extreme southwestern part of Africa, where a number of significant archaeological sites preserve evidence for the ways of life of earlier modern humans. The region that comprises the southwestern coast of South Africa needs separate investigation because it is unique in terms of both its Mediterranean climate and Fynbos vegetation, one of the world's six floral kingdoms.

Based on information from the literature, I expect that: $\delta^{13}C$ will inform us mainly about the proportions of C_3 and C_4 vegetation; $\delta^{15}N$ will vary based on the plant nitrogen isotope values; and $\delta^{18}O$ will vary mainly according to moisture availability. The details of these relationships are, however, not well understood and elucidating these patterns is the major aim of this thesis. Establishing an isotopic database for modern fauna will provide a key tool in the reconstruction of palaeoclimates and palaeoenvironments. The limited number of contemporary animals analysed prior to this study have limited the assessment of the degree of natural variation in stable isotope values within a region or biome – a prerequisite for assessing the significance of apparent differences among isotope values of archaeological and fossil faunal assemblages. Isotopic analyses of archaeological fauna will help to reveal the palaeoenvironmental context for the emergence of modern humans in this region.

In Chapter 1, I provide a description of the broader global environmental changes in order to provide the context into which my work will fit. I also explain my research objectives and describe the scope of the study. Finally, I outline the organisation of the thesis itself.

1.2 Background: Global climate

The study of shifting climatic and environmental patterns is crucial to understanding species adaptation and evolution. In order to ascertain past climatic and environmental conditions, researchers have studied various proxies such as ocean sediments, fossil pollen, tree-ring analysis and animal remains (including teeth and bones) (Macphail and Cantrill, 2006; Hall *et al.,* 2008; Stager *et al.,* 2009; Brophy *et al.,* 2014). With respect to the examination of animal remains, stable light isotope ratios are useful for the study of palaeoenvironments, as isotopic ratios are preserved in teeth and bones and reflect the types of foods consumed by the animal (Ambrose, 2002; Brookman and Ambrose, 2013; Lee-Thorp and Sponheimer, 2015; Lehmann *et al.,* 2016; Naidoo *et al.*, 2016).

Sediment cores extracted from the ocean seabed provide invaluable data, including foraminifera with $\delta^{18}O$ that can provide details about the temperatures of the ancient ocean. From such data, it has been determined that there was a peak in sea-surface temperature around 55 million years ago (mya), after which the temperature started to fall (Marlow *et al*., 2000; McCarthy and Rubidge, 2005). Ice accumulated in Antarctica, possibly for the first time, around 40 mya. At approximately 35 mya, the Drake Passage opened up between Antarctica and South America, causing the circum-Antarctic circulation to form, which isolated Antarctica. With the northward movement of Australia, the Southern Ocean increased in size and caused a reduction of the flow of warm Pacific Water into the Indian Ocean, causing a dramatic cooling of the Southern Ocean. A strong high pressure system became established over the South Atlantic Ocean and eventually the Benguela Current off the west coast of Southern Africa was formed by about 14 mya (McCarthy and Rubidge, 2005).

On the African continent, subtropical and tropical environments characterised most of the Miocene (22-6 mya). Global cooling meant that such conditions gave way to more temperate and seasonal environments during the late Miocene (deMenocal, 1995; deMenocal, 2004; Dupont *et al*., 2013). The cooling of the ocean influenced shifts in terrestrial climate and environment because previously, moisture had been drawn to the southwestern region of the continent from both the east and the west. With the development of the cold Benguela current, the result was a reduction in moisture coming off the Atlantic Ocean in the west (Marlow *et al*., 2000; Dupont *et al*., 2005). This change caused the western part of the continent to become much more arid resulting in a strong rainfall gradient with more precipitation in the east (McCarthy and Rubidge, 2005). Uplift of the eastern part of the interior meant the rainfall gradient became more extreme as much of the moisture coming from the east was lost as the air moved up the escarpment towards the western part of Southern Africa (McCarthy and Rubidge, 2005).

Although C_4 grasses evolved for the first time 25-35 mya (Sage, 2004; Edwards *et al.*, 2010), it was only about 7-8 mya that they expanded to form grasslands throughout the world (Cerling *et al*., 1997; Ehleringer *et al.*, 1997; Retallack, 2001; Edwards *et al.*, 2010). While these grasses spread across the summer rainfall areas, grasses in the winter rainfall area were mostly C_3 (Franz-Odendaal *et al.,* 2002). There is still some debate as to the reason for the major expansion of C_4 grasses. Since C_4 grasses are more efficient at fixing CO_2 than C_3 grasses, it was originally suggested that low concentrations of CO_2 were responsible for this global spread (Cerling *et al.*, 1997). However, there is little evidence for significant changes in CO_2 levels over the period of the C_4 expansion (Cerling *et al*., 1997; Pagani *et al.*, 1999), making this an unlikely reason. It is more likely that the cause was an event such as a tectonic event that led to increased aridity or a change in the seasonality of precipitation (Pagani *et al*., 1999).

During the Pleistocene (ca. 2.6 mya to 11.7kya years ago) the climate was much more unstable and marked by repeated glacial cycles (McCarthy and Rubidge, 2005). It was also during this time that the genus *Homo* evolved in Africa (Antón *et al.,* 2014). Evidence of palaeotemperatures from this time period have been obtained from ice cores extracted from Antarctica and Greenland as well as from sediment cores taken off both the east and west coasts of South Africa (McCarthy and Rubidge, 2005). The severe climatic changes during glacial/interglacial periods had major impacts on fauna and flora, and probably impacted the evolution of the genus *Homo* as well.

Around 1.7 mya *Homo erectus* and *Homo ergaster* appeared, bringing with them the first evidence of controlled fire (Organ *et al*., 2011); it is thought that archaic *Homo sapiens* evolved from this lineage. Remains of archaic *Homo sapiens* have been found at Florisbad in the Free State (Kuman *et al.*, 1999), and at Hoedjiespunt (Berger and Parkington, 1995; Stynder *et al*., 2001) in the Western Cape. Modern *Homo sapiens* (which some authorities call *Homo sapiens sapiens*) appears after 200 000 years ago (Stringer and Buck, 2014). In South Africa, important remains of *Homo sapiens sapiens* have been found at Klasies River (Singer and Wymer, 1982; Rightmire and Deacon, 1991; Pearson and Grine, 1996; Grine *et al*., 1998; Rightmire and Deacon, 2001; Grine, 2012), Border Cave (Beaumont *et al.*, 1978) and Hofmeyr Cave (Grine *et al.*, 2007), and small fragments of bone and isolated teeth have been recovered from many other sites. During the Middle Stone Age (MSA), advanced forms of tool-use emerged as well as the appearance of evidence for symbolism, personal ornamentation and other indicators of complex behaviours (Wadley, 2001; Henshilwood *et al*., 2002; Henshilwood *et al.*, 2009; Wadley, 2013). The environment is likely to have played a role in the development of modern humans and their advanced cognitive capacities; the importance of this role is not yet well understood (Stringer, 2016). Crucially important evidence of the Pleistocene environment comes from sites such as Langebaanweg, Elandsfontein and Hoedjiespunt where carbon isotopes indicate a winter rainfall regime was in effect from at least 5 mya, as it is today. Since the carbon isotope values vary from site to site, there is uncertainty as to what small differences in $\delta^{13}C$ mean within in the broad winter rainfall, or C_3 dominated, environment.

The Holocene (from 11 700 years ago to the present) has been a period of increased climate stability with the persistence of short periods of warming and cooling. It is thought that the advent of the Holocene facilitated a change in human subsistence practice from a mobile hunter-gatherer lifestyle to a preference for increased sedentism with the widespread adoption of farming within the last 10 000 years.

Archaeological sites contain records of past climates and environments in the form of faunal and floral remains and sediments. Unlike marine cores, where records may often be time-averaged over long periods, well-dated terrestrial archaeological sites can yield highly-resolved palaeoenvironmental datasets. In addition, palaeoenvironmental data from archaeological sites can be directly correlated with archaeological evidence for human behaviour derived from these same sites. Gaining a better understanding of environmental change, demonstrated through evidence from archaeological sites, can provide insights into some of the factors that may have influenced our evolution.

1.3 Objectives and scope

This study provides a framework for quantifying the environmental correlates of the shifts in stable isotope values evident in archaeological datasets. Specifically, it measures the relationship between environmental variables such as precipitation, relative humidity and temperature, all of which influence the isotopic ratio in plants and in the animals that consumed those plants. Most studies of isotope ecology in Africa have been done in summer rainfall regions (generally savannahs) of Eastern and Southern Africa (Ambrose and DeNiro, 1986; Cerling et al., 2004; Codron and Brink, 2007; Codron and Codron, 2009; Codron et al., 2006a; Codron *et al.,* 2007a). An understanding of these relationships in other environments, including the winter rainfall areas of the southwestern Cape, is currently weak (Hare and Sealy, 2013). This project therefore focusses on the winter rainfall zone with an emphasis on an environment in which trees, shrubs, bushes and also the vast majority of grasses photosynthesise by means of the C_3 pathway. I do not, therefore, expect to see the major differences in the carbon isotopic ratios between C_3 and C_4 consumers since most of the grasses in these regions will also be C_3. Therefore, this thesis will also explore more subtle variation in carbon, nitrogen and oxygen isotopes arising from climatic and environmental differences within areas in Southern Africa that receive a significant proportion of their rain in winter (i.e., the winter and all-year rainfall zones), as well as immediately adjacent regions.

The primary objective of this thesis is to study the distribution of stable C, N and O isotopes across natural contemporary ecosystems in order to produce a baseline for archaeological reconstructions. The aim is to test the nature and extent of the correlation between meteorological factors and the carbon, nitrogen and oxygen isotopic values of fauna in the contemporary winter and year-round rainfall zones. These relationships have not previously been investigated in a systematic manner in South African C_3 environments.

The study focusses on larger mammals (body mass > 4 kg) with known provenance in areas of natural or near-natural vegetation. Most animals were sourced from provincial and national parks and game reserves but in some cases from private properties. Samples of bone and tooth enamel were taken from each animal, where possible, in order to ascertain the isotopic relationships between the two tissues and between each tissue and the environmental factors in which the animal lived. This dataset will, therefore, contribute to a better understanding of isotope systematics in large mammals. The results of this study can then be applied to archaeological sites not only within the winter and year-round rainfall zones of South Africa, but further afield as well.

$^{13}C/^{12}C$ (or $\delta^{13}C$) of fauna has been used mainly to distinguish between the proportions of C_3 and C_4 plants consumed (Vogel, 1978). In addition, $\delta^{13}C$ values of fauna can reflect variations in $\delta^{13}C$ of C_3 plants in accordance with environmental conditions (Diefendorf *et al*., 2010). The ways in which environmental variables interact to produce patterns of isotopic variation is currently a major topic of research, with researchers developing 'isoscapes' through mapping existing data and also modelling expected values on a range of scales including both continental and global (Schoeninger, 2010; West *et al.*, 2010; Bowen, 2010). Due to the winter rainfall climate system that characterises southwestern Africa, such large-scale mapping and modelling projects have thus far not provided the level of detail that is needed for palaeoenvironmental and archaeological work in this area. We currently lack an understanding of the nature of and extent to which climatic variations affect $\delta^{13}C$ values, making it difficult to interpret small shifts seen in some archaeological and palaeontological datasets (Hare and Sealy, 2013; Lehmann *et al*., 2016). This study will provide an adequate modern baseline from which to make sense of these subtle variations.

Oxygen isotope systematics ($^{18}O/^{16}O$ or $\delta^{18}O$) of fossil fauna are more complex and somewhat less well understood than other isotope systematics. $\delta^{18}O$ of fauna depends on food and drinking water, as well as aspects of animal physiology (Lee-Thorp, 2002; Levin *et al.,* 2006; Lee-Thorp, 2008). Elsewhere in Africa, differences in $\delta^{18}O$ between arid adapted species and those that regularly drink water provide an index of aridity that is useful as a palaeoenvironmental indicator (Levin *et al.,* 2006). This study will explore the applicability of this method in the winter and year round rainfall regions. It is anticipated that these results will contribute to studies of climate change in Southern Africa, thereby contributing to our understanding of aspects of human evolution in the region.

Foliar $^{15}N/^{14}N$ (or $\delta^{15}N$) varies across environmental gradients (Amundson et al, 2003; Craine et al., 2009; Murphy and Bowman, 2009). Faunal $\delta^{15}N$ varies across environmental gradients in the same way as foliar $\delta^{15}N$ (Heaton *et al.*, 1986; Gröcke *et al.*, 1997; Pate and Anson, 2008; Smiley *et al.,* 2015). There is debate around the factors that control variation in $\delta^{15}N$ in fauna (Sealy *et al.,* 1987; O'Connell *et al.*, 2012). What is not well understood is the importance of metabolic drivers in particular (O'Connell *et al.*, 2012). This is particularly true for the winter rainfall region of southern Africa. The present study therefore aims to explore correlations between $\delta^{15}N$ in fauna and environmental variables in this area.

Three main questions will form the basis of the current study:

1. In what way and to what degree do $\delta^{13}C$ and $\delta^{18}O$ of faunal tooth enamel, and $\delta^{13}C$ and $\delta^{15}N$ of bone collagen vary with changes in environmental variables (principally precipitation, temperature and/or aridity) in areas that are dominated by C_3 vegetation?

2. What is the relationship between isotopes from different skeletal elements within one individual? Firstly, between the stable carbon isotope ratios in tooth enamel and bone collagen and secondly, where hemi-mandibles/maxillae are available, between teeth along the tooth row. This information will provide a more detailed picture of how isotopic values vary within an individual.

3. How best can we use the modern baseline generated in this study to help us interpret the differences observed in isotopic signals of faunal assemblages from archaeological sites?

In summary, this work will document, for the first time, natural variation in stable C, N and O isotopes in animals from the C_3 winter rainfall biome of southern Africa. There have been some previous small-scale studies of this topic, but a coherent overall picture is lacking. The primary objective of this research is to test the nature and extent of the correlation between meteorological factors (such as temperature, relative humidity, precipitation) and carbon, nitrogen and oxygen isotopic values of contemporary fauna in this region. The study will focus on the areas in southern Africa that receive all or a significant proportion of their rain in winter (i.e., the winter and all-year rainfall zones). Faunal samples derive mainly from protected areas where indigenous animals still feed on natural vegetation. This study will therefore explore the role of environmental and climatic factors in determining the isotopic ratios of selected faunal species in predominantly C_3 environments. Information resulting from this analysis can then be used to interpret archaeological datasets more accurately with respect to the identification of climatic shifts in the past.

1.4 Structure of the thesis

Chapter 1 provided a brief background to the thesis, outlining the reasons why this work was undertaken and the goals of the study. Chapter 2 describes stable light isotope systematics and how this method has been used to answer questions related to the palaeoenvironments of Southern Africa. In particular, the chapter deals with isotopic variation in plants and how this is transmitted to the animals that consume these plants. Patterning in stable light isotopes in mammals will also be discussed in Chapter 2.

Chapter 3 describes the research area and relevant environmental data and Chapter 4 provides a review of the sampling techniques and methods. Chapter 5 reports the isotopic results for enamel carbonate ($\delta^{13}C_{enamel}$ and $\delta^{18}O_{enamel}$) and Chapter 6 reports those for bone collagen ($\delta^{15}N_{collagen}$ and $\delta^{13}C_{collagen}$). Chapter 6 also assesses intra-individual variation by comparing the carbon isotope values of tooth enamel and bone collagen in each individual. Chapter 7 discusses the patterns found in this dataset with reference to previously published studies and concludes with some suggestions for future research.

Chapter 2: Review of the use of light stable isotopes

2.1 Introduction

Over the last few decades, the analysis of light stable isotopes in mammal bioapatite and collagen has been used extensively for dietary and environmental reconstructions (Ayliffe and Chivas, 1990; Ambrose and Norr, 1993; Bryant *et al.,* 1996; Adams and Sterner, 2000; Cerling *et al.,* 2008; Sponheimer and Cerling, 2013). Isotopic ratios in body tissues derive from foods consumed by the individual and can therefore be used to track aspects of the environment in which the animal lived (Ambrose, 1991). Habitat and digestive physiology may, however, complicate these diet-to-tissue relationships (Codron *et al.*, 2006a; Codron *et al.*, 2011) . As the understanding of isotope patterning has increased, it has become clear that animal behaviour (dietary selection) and physiology significantly affect tissue isotope values and that this varies between species (and perhaps even within species) (Codron *et al.*, 2011). For this reason more work on modern animals is required before it is possible to provide effective interpretations of archaeological and fossil assemblages.

This chapter will first summarise relevant aspects of the composition and formation of bone and tooth enamel, which are important in interpreting the isotope measurements. It will then briefly review the literature on carbon, oxygen and nitrogen isotope variation in food webs, paying special attention to studies of large mammals in Africa.

2.2 Structure and composition of calcified tissues in animals

The animal tissues most commonly analysed in palaeoenvironmental studies are bones and teeth because they can survive for long periods of time and are therefore the most common vertebrate tissues found in archaeological and fossil assemblages. They are biomineralised materials consisting of an inorganic mineral component (referred to as bioapatite), a substituted calcium phosphate apatite. From bioapatite $^{18}O/^{16}O$ can be determined from phosphate, and $^{13}C/^{12}C$ and $^{18}O/^{16}O$ from the substituted carbonate. The organic component consists mainly of the protein collagen, in which $^{2}H/^{1}H$, $^{18}O/^{16}O$, $^{34}S/^{32}S$, $^{13}C/^{12}C$ and $^{15}N/^{14}N$ can be measured.

2.2.1 Teeth: composition, formation and remodelling

A tooth consists of the crown and one or more roots (Hillson, 2005; Ungar, 2010). Teeth have three layers: the first is the pulp chamber where the nerves and blood vessels are located; the second layer is the dentine (Hillson, 2005) (Figure 2.1). The crown is covered by a layer of enamel, a bioapatite mineral, and the roots are coated with cementum, a bone-like tissue (Ungar, 2010).

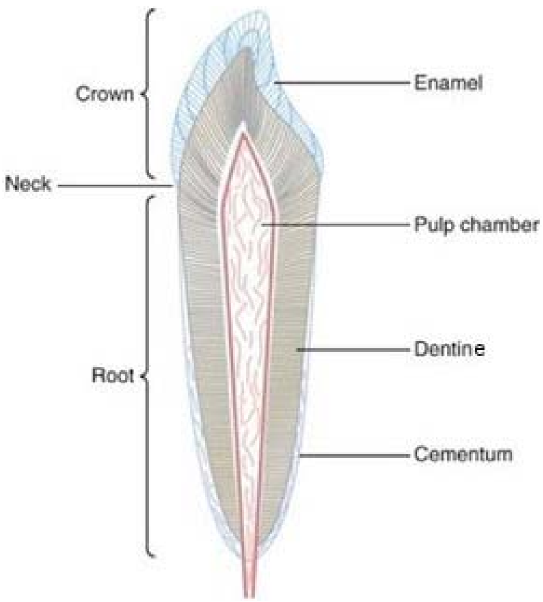

Figure 2. 1 Tooth structure depicting position of enamel, cementum, dentine and pulp (Adapted from (Hillson, 2005)).

Most mammals have four types of teeth, i.e., incisors, canines, premolars and molars (Ungar, 2010), with each having a different function. A generalised mammalian permanent dental formula (a method for summarising dentition) is:

$i\frac{3}{3}\ c\frac{1}{1}\ p\frac{4}{4}\ m\frac{3}{3}$

where the letters indicate teeth types (i = incisors, c= canines, p = premolars, m= molars), the superscript numbers are the counts for upper teeth and the subscript numbers are the counts for lower teeth on each side of the mouth (Hillson, 2005). Not all mammals have exactly this dental formula, but all are similar (e.g., Fig. 2.2). For example, humans have only two incisors and two premolars.

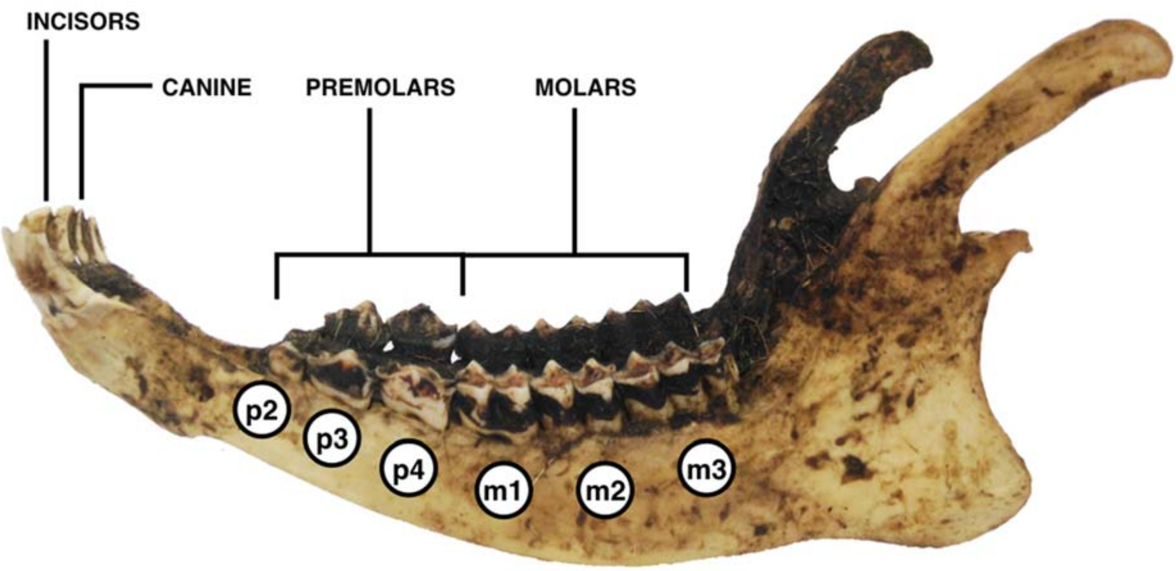

Figure 2. 2 Springbok (*Antidorcas marsupialis*) mandible to illustrate ungulate dentition: Incisors, Canines, Premolars and Molars (Photo: J. Luyt).

Most mammals have two sets of teeth: deciduous and permanent. This is thought to be related to growth and the need for the dentition to scale up with increasing body size. Deciduous teeth are much smaller and the enamel is much thinner than in permanent teeth (Hillson, 2005). The timing of the replacement of the deciduous dentition varies among mammal species, with some having their permanent teeth at birth while in some primates (like humans), permanent teeth continue to erupt into early adulthood (Ungar, 2010). Other mammals, such as elephants and rodents, have teeth that grow continuously throughout the animal's life (euhypsodonty or ever-growing teeth) (Ungar, 2010).

Enamel, which is the hardest substance in the body (Pasteris *et al.*, 2008; Ungar, 2010), consists of complex combinations of uniformly wide, well-oriented crystals of hydroxyapatite ($Ca_{10}[PO_4]_6[OH]_2$, a mineral group found only in mammalian tissues (Swindler, 2002) packed into an organic matrix (Boyde, 1967; Pasteris *et al.*, 2008). Mature enamel is comprised primarily of inorganic calcium phosphate (96%), predominantly in the form of hydroxyapatite (Pasteris *et al.*, 2004; Hillson, 2005), but is highly substituted. The remainder of the enamel consists of approximately 1% non-collagenous protein and 3% water (Figure 2.3).

Dentine is made up of approximately 70% hydroxyapatite, 20% collagen and other proteins, and 10% water (Ungar, 2010). Dentine has a lower mineral content (Figure 2.3) and is thus softer than enamel. Primary dentine is laid down at the time of tooth formation, shortly after the commencement of enamel mineralisation. Secondary dentine forms very slowly over the lifetime of the animal and is usually associated with a reduction in the number of functioning odontoblasts (Zilberman and Smith, 2001). Unlike enamel, dentine can repair itself, which leads to the formation of tertiary dentine. An example of the formation of tertiary dentine would be when enamel wears thin and new dentine forms as a localised response to thinning to aid in shielding the exposed surface of the tooth or teeth (Zilberman and Smith, 2001; Ungar, 2010).

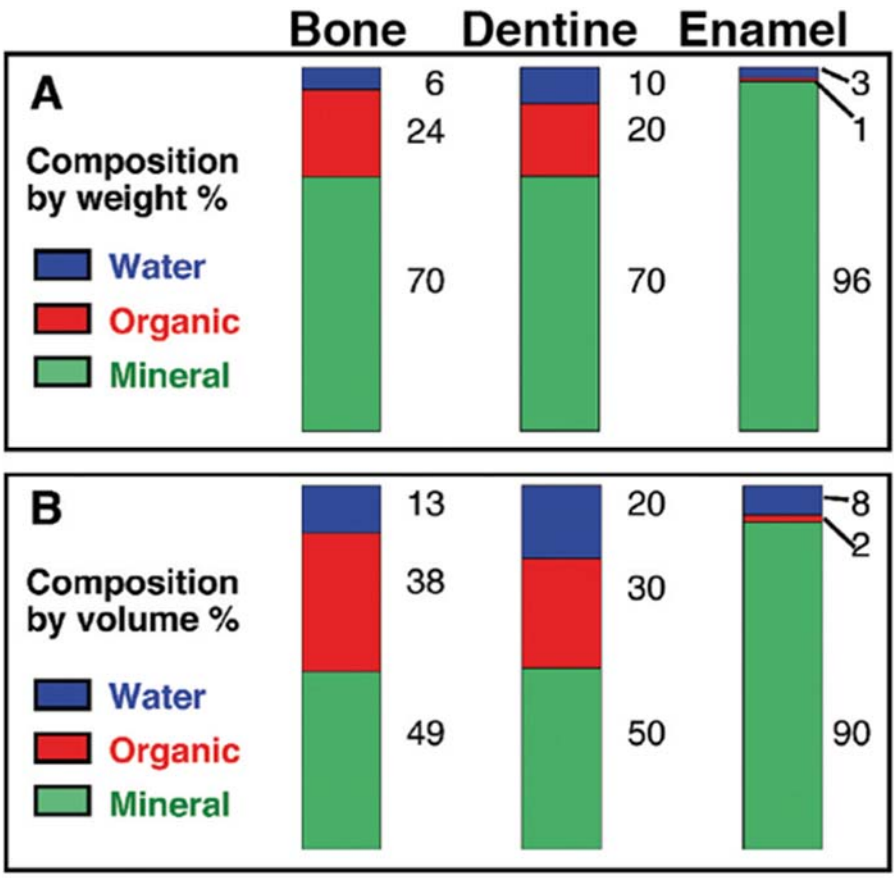

Figure 2. 3 The major components of enamel, dentine and bone. A: Composition by weight. B: Composition by volume (From: (Pasteris *et al.*, 2008, Fig. 1, p. 98)).

Tooth formation takes place early in the life of most mammals. In species that do not have continuously growing teeth, dental tissue, and therefore the isotopic composition of teeth, reflects the diet consumed during the early part of an individual's life. Teeth start to form at the occlusal surface and proceed towards the root. Enamel grows incrementally, a fact which is useful in studies that investigate patterns of seasonal variability during the time teeth were forming (Balasse *et al.*, 2002).

Enamel formation (amelogenesis) takes place in two stages: organic matrix secretion and mineralisation (Ungar, 2010). The enamel matrix comprises about one third protein, one third minerals and a third water. The ameloblasts first secrete the proteins (Pasteris *et al.*, 2008). This initial stage of deposition is mineral-poor but is followed by substantial mineral accumulation during the formation of hydroxyapatite (Passey and Cerling, 2002). As enamel matures, the protein and water is slowly removed until mature enamel contains less than 1%

protein. Mature enamel crystallites then pack together, forming a dense, crystalline mass. The mineral content of enamel increases even after the final thickness of the enamel is reached (Passey and Cerling, 2002), with about two thirds of the enamel being added after the initial formation of the crown. Dental enamel is usually fully formed before the tooth erupts into the oral cavity yet the process of mineralisation varies slightly between species. For example, Hoppe *et al.* (2004) found that enamel layers in equid molars takes longer to mineralise than had previously been assumed, largely because the enamel continues to mineralise for up to 12 months after each tooth starts to erupt. There is no reformulation or subsequent addition of enamel; it is never remodelled or repaired.

The sequence in which teeth emerge in mammals is highly patterned. In most mammals, the deciduous set of teeth is fully erupted before the permanent set begins to erupt (Smith, 2000). The sequence of each stage from initial mineralisation, crown completion, root completion and emergence is similar across all species, with first molars forming and erupting first and third molars emerging last (Swindler, 2002). The sequence of mineralisation and eruption of the permanent teeth is generally M1, I1, I2, C, P3, P4, M2 and M3, a sequence which varies slightly in order depending on the species (see Figure 2.4 below). M1 erupts as early as the first month of life in some ungulates or as late as 6 years in humans (Smith, 2000) (Figure 2.4). The time span over which eruption takes place depends on the rate of growth or maturation of the animal (Smith, 2000); permanent teeth begin to erupt earlier in small animals compared with large ones. For example, in larger bovids (such as *Connochaetes, Tragelaphus* and *Bison*) the M1 erupts only at about 6 months (Smith, 2000). However, as always, there are exceptions. The eruption sequence of the giraffe is more rapid than may be expected given the animal's size (often weighing 500 kg or more) while the 2 kg *Procavia* (the rock hyrax) has a much slower eruption than predicted (Smith, 2000). With respect to upper and lower dental eruption, the difference in timing between the maxilla and mandible is marginal, with the mandibular tooth emerging slightly earlier (Smith, 2000).

Table 2. 1 Eruption sequence of mandibular teeth for A) primates and insectivores and B) ungulates A) (Smith, 2000, Figure 15.4, p. 217) B) (Smith, 2000, Figure 15.5, p. 218).

A: Primates and insectivores

Species	Time of eruption of M1 in years	Eruption sequence from left to right														
Urotrichus		M1				M2						M3	PP	P	I	
Tupaia	0.09	M1				M2						M3	PIP	I	P	I
Lemur	0.34	M1				M2			P	P	P	M3				
Aotus	0.36	M1				M2				I		M3	I	P	PP	
Saimiri	0.37	M1				M2	I	I	P	PP		M3				
Eulemur	0.42	M1				M2					P	M3	P	P		
Varecia	0.48	M1				M2				PP		M3	P			
Alouatta		M1		I	I	M2	PP	P				M3				
Cercopithecus	0.83	M1		I	I	M2	P	P				M3				
Cebus sp.	1.1	M1		I	I	M2	P	P				M3				
Macaca	1.4	M1		I	I	M2	P	P				M3				
Papio	1.6	M1		I	I	M2	P	P				M3				
Pan	3.2	M1		I	I	M2	P	P				M3				
Homo	6.3	M1	I	I	P	M2	P					M3				

B: Ungulates

Species	Time of eruption of M1 in years	Eruption sequence from left to right													
Antidorcas	0.08	M1				M2					M3	I	II	P	P
Antilocapra	0.17	M1				M2					M3	I	P	P	IPI
Rangifer	0.17	M1			I	M2				II	M3	PP	P		
Odocoileus	0.18	M1			I	M2				II	M3	PP	PP		
Muntaicus	0.2	M1				M2				I	M3	I	PP	PI	
Hemitragus	0.21	M1				M2				I	M3	I	P	PPI	
Sylvicapra	0.23	M1				M2					M3	PP	P	I	II
Aepyceros	0.33	M1				M2				I	M3	I	PP	IP	
Okapia		M1				M2				I	M3	I	PI	PP	
Cervus	0.33	M1				M2			I	I	M3	IPP	P		
Tayassu	0.4	M1				M2	I	I	P	PP	M3				
Connochaetes	0.46	M1				M2				I	M3	I	P	PI	
Sus	0.47	M1				M2	I	P	PP	I	M3				
Taurotragus	0.53	M1				M2				I	M3	II	PP	P	
Bison	0.54	M1				M2				IP	M3	P	I	IP	
Procavia	0.54	M1		I	I	M2	PP	P			M3				
Giraffa	0.66	M1				M2				I	M3	P	PP	II	
Equus	0.88	M1				M2			I	PP	M3	I	PI		
Hippopotamus	~2	M1		I	I	M2	PP	P			M3				
Ceratotherium	2.75	M1				M2	P	P			M3				

In summary, enamel, dentine and cementum cannot be remodelled following formation because they lack a blood supply. Enamel is formed (mineralised) early on in life with tooth eruption occurring at various stages during the life of an animal. In species that do not have continuously growing teeth, dental tissue, and therefore the isotopic composition of teeth, reflects the diet consumed during the early part of an individual's life.

2.2.2 Bone: composition, formation and remodelling

Bone is a living tissue in which cells are constantly replaced and repaired over time. Bone is a composite material which includes poorly crystalline bioapatite integrated with an organic matrix made up of multiple helical fibrils (Aiello and Dean, 1990; Currey, 2002; Koch, 2007; Pasteris *et al.*, 2008; Lee-Thorp, 2008); its fine structure varies with age (Aiello and Dean, 1990). The composition of bone by weight (Figure 2.3) is about 20-30% organic and consists mainly (85-90%) of the protein collagen with a small proportion of non-collagenous proteins (Fratzl *et al.*, 2004); about 45-70% is inorganic and consists of the bioapatite mineral analogous to hydroxyapatite; and about 10% consists of water.

Long-bones and many other skeletal elements consist of dense external (or cortical) bone and spongy interior (or cancellous) bone. Initial bone formation occurs *in utero* (Scheuer *et al.*, 2000). The growth of osseous material is a complex process which involves ossification of the cartilage (in the case of long bones) as well as accretionary growth (Koch, 2007). Ossification (bone tissue formation) is the process of laying down new bone material by cells called osteoblasts (Boskey, 1981). There are two major processes that create bone: either intramembranous ossification for flat bones (such as the skull, jaw and clavicle) or endochondral ossification for long bones (Koch, 2007). There are four major steps that occur during the process of ossification. Firstly centrally located stem cells specialise into osteoblasts, forming the ossification centre. In the second step, the osteoblasts start to secrete the fibres (proteins) that make up the bony matrix. The third step is the formation of the spongy bone and the concentration of the blood vessels. The final step is the osteoid condensing to form lamellar bone (compact bone) around the spongy bone (on both sides). During the growth of long bones, the length of the bone as well as its diameter increases in size.

Associated with the development of lamellae, modelling is part of bone growth, a process that changes the mass and architecture of bone by adding and removing material from select surfaces. Over time, lamellae are removed from bone during modelling so that by the time the skeleton is fully mature, it includes layers of lamellae of varying ages. After attaining initial maturity, bone modelling reduces drastically (Fratzl *et al.*, 2004; Robling and Stout, 2007; Hedges *et al.*, 2007). Unlike modelling, remodelling of bone occurs through a process of removing discrete portions of bone. During remodelling, osteoclasts resorb existing bone and lay down new material, causing the bone to be reformulated over time (Robling and Stout, 2007; Pasteris *et al.*, 2008). This process of resorption/formation of new bone is referred to as turnover.

The turnover rate of bone depends on the age, diet and health of the individual (Pasteris *et al.*, 2008) and also varies between species, individuals and different skeletal elements (Hedges *et al*., 2007; Robling and Stout, 2007). Compact bone turns over more slowly than cancellous bone and thus contains tissue laid down over a longer period. The turnover rate for human mid-shaft femoral bone ranges from 10-30% per year in the teen years to 1.5-4%

in individuals aged 20- 80 years (Hedges *et al*., 2007). The isotopic composition of such bone thus reflects a longer term average of the foods eaten during that individual's lifespan than is the case for tooth enamel (Lee-Thorp, 2008).

The principal organic component of bone is a fibrous protein called collagen (Weiner and Wagner, 1998). There are many types of collagen but the type found in bone, dentine, skin and tendons is the same (Currey, 2002). This type of collagen has a characteristic spectrum of amino acids, including hydroxyproline, which make it unique. The amino acids in collagen are extremely ordered, with the most abundant type being glycine (approximately 33%) and proline and hydroxyproline together constituting another 20-25% of the total (Schwarcz and Schoeninger, 1991). The regular amino acid sequence accounts for both the structural integrity and the triple helical form since only glycine is small enough to fit in the centre of the triple helix (Schwarcz and Schoeninger, 1991). The amino acids join to form spiral chains, three of which twist together into a triple-helix macromolecule that pack together to form fibrils. When bone forms, the matrix of collagen fibrils is laid down first and then apatite crystals are seeded into the gaps between the fibrils (Hillson, 2005).

The inorganic component in bone is also a biological apatite (analogous to hydroxyapatite), but it is highly substituted with poorly formed (small and distorted) crystallinity (Pasteris *et al.*, 2008). The processes of formation of bone apatite (which is not hydroxylated) and enamel apatite (which is) are slightly different (Pasteris *et al*., 2004). The carbonate in apatite is derived from dissolved CO_2 in the blood plasma and thus represents the total metabolic carbon pool (i.e., diet) (Schwarcz and Schoeninger, 1991). Although bone apatite survives much longer than collagen in archaeological and fossil bones, it is a reactive substance, susceptible to diagenesis (Lee-Thorp, 2008). For this reason, many researchers in recent years have tended to avoid isotopic studies of bone apatite, preferring to analyse tooth enamel. Nevertheless, renewed work indicates that the analysis of bone apatite can be a viable avenue of research (Santana - Sagredo *et al*., 2015a; Santana - Sagredo *et al.*, 2015b) which is significant given that collagen does not usually survive beyond 50 000 years (Van Klinken, 1999). Bone apatite can provide a longer-term integrated signal of an animal's diet than enamel apatite as it forms and re-forms over the entire lifespan of the individual. This is especially relevant in older individuals.

In summary, as with enamel, bone formation begins *in utero* but unlike enamel, it is then remodelled over the animal's lifespan, meaning that the isotopic ratios in bone will reflect diet over a much longer time period than those in enamel.

2.2.3 Suitability as analytical substrates

Dental enamel consists almost entirely of highly crystalline minerals with very little (~1%) organic material. Therefore, decomposition of organics does not open up significant spaces for exogenous materials to penetrate the enamel. This would lead to contamination and the possibility of structural re-organisation, as in the case with bone. In addition, the large size of enamel crystals allows for fewer substitutions (Koch, 2007; Pasteris *et al.*, 2008); substitutions tend to impose strain on the crystal lattice, which increases solubility. As a consequence, enamel is far less susceptible than bone to post-depositional alteration. Enamel is therefore usually the best-preserved tissue and is frequently the analytical substrate of choice for isotopic and other analyses.

Bone contains much more protein (about 20-30%), mainly in the form of collagen. In many environments, protein tends to decay relatively quickly after the animal's death, making bone considerably more porous and susceptible to changes to its mineral structure (diagenesis) (Kohn and Cerling, 2002). In hot climates, diagenetic alteration has been observed in exposed bones after only a few years (Tuross *et al.*, 1989). An additional complicating factor is that different types of bone have different levels of porosity. For example, cancellous or spongy bone has a much greater surface area and is therefore more susceptible to alteration than cortical or compact bone (Sealy *et al*., 1991). Due to this reduced preservation potential, bone collagen is generally used for isotopic studies of more recent chronological periods (Lee-Thorp 2008).

Carbon and oxygen isotopes in both bone and enamel have been widely used in palaeo studies. While bone collagen reflects mainly the isotopic ratios of dietary protein, bone apatite is thought to be more reflective of diet as a whole. Studies have shown that $\delta^{13}C$ and $\delta^{18}O$ in bone apatite and enamel apatite are off-set from one another, even for bone and enamel forming at the same time (Howland *et al*., 2003; Passey *et al*., 2005; Warinner and Tuross, 2009; Webb *et al.*, 2014). Enamel is more enriched in ^{13}C than bone apatite (Warinner and Tuross, 2009; Webb *et al.*, 2014). Oxygen is present in two locations in apatite: phosphate (PO_4^{3-}) as well as carbonate (CO_3^{2-}). When oxygen isotopic systematics were first studied, most studies focussed on the phosphate oxygen since the P-O bond was thought to be stronger than the C-O bond in carbonate. However, $\delta^{18}O$ in phosphate and carbonate have been found to be highly correlated in enamel apatite (Bryant *et al*., 1996; Iacumin *et al*., 1996; Sponheimer and Lee-Thorp, 1999a; Webb *et al.*, 2014), and thus most studies have moved to measure the "easier" carbonate (CO_3^{2}).

2.2.4 Intra-animal variation

Animal tissues record the diet of the individual over the time of tissue formation. By looking at intra animal variations, much can be learnt about that animal. Teeth reflect diet in early life while bone is constantly remodelled over time, representing a much longer time period. Other tissues such as muscle, hair and faeces (which fall outside the scope of this thesis) represent much shorter time periods. Differences between the $\delta^{13}C$ in bone and teeth is discussed in detail under the 'Carbon' section below (section 2.4).

As each tooth forms and mineralises, it would be representative of that period in the animal's life (White *et al*., 2000; Balasse *et al*., 2001; Balasse, 2002; Zazzo *et al*., 2002; Murphy *et al.*, 2007a; Zazzo *et al*., 2012; Tornero *et al*., 2016a; Tornero *et al*., 2016b); measurements of multiple teeth that erupt at different times enables researchers to track possible changes of diet (White *et al.,* 2000; Balasse *et al.,* 2001). Differences between teeth that form very early in life, such as the M1 which mineralises pre-weaning, and other teeth that form post weaning could be attributed to dietary differences between very young animals that are still suckling compared with older animals that are not. However, since the lipid content of milk is very low in ungulates (about 3.7%), some authors have argued that the weaning effect will be small (Balasse, 2002). Others have attributed differences in the diet-to-enamel fractionation between M1 and M3 to the weaning signal (Murphy *et al.*, 2007a). Several studies have found M1 to be depleted in ^{13}C relative to the M3 (Hobson and Sease, 1998; Gadbury *et al*., 2000; Zazzo *et al*., 2002). Zazzo *et al.* (2002) reported variations in $\delta^{13}C$ in tooth enamel in M1, M2 and M3 ranging between 0.9‰ and 1.9‰ (for five archaeological specimens of *Tragoportax afghanicus*). Wang *et al*. (2008) reported a range of 0.6 to 4.8‰, slightly larger than that found by Zazzo *et al.* (2002). The corresponding ranges for $\delta^{18}O$ are are 0.4‰ to 3.7‰ (Zazzo *et al*., 2002) 2.0‰ to 10.8‰ within one individual (Wang *et al*. 2008). Tornero *et al.* (2016) reported $\delta^{18}O$ ranges of 2.9‰ to 4.4‰ for archaeological domestic sheep.

2.3 Light stable isotopes in nature

Many elements occur naturally in more than one isotopic configuration; they have the same numbers of protons and electrons but differ in the number of neutrons. Such a configuration results in atoms with different weights having the same chemical properties (Sharp, 2007). The lighter elements in the periodic table, especially D/H, $^{13}C/^{12}C$, $^{15}N/^{14}N$, $^{18}O/^{16}O$ and $^{34}S/^{32}S$, tend to react more rapidly than heavier ones through naturally-occurring processes such as evaporation or diffusion. Many enzymes will bind more readily with one isotope (usually the lighter one) over the other, causing the ratio of the isotopes to vary in plants and animals to an extent that can be measured. This shift in the proportion of heavy to light isotopes is termed 'fractionation[1]'.

Notation

Due to the fact that we are concerned with small differences in the absolute heavy to light isotope ratio, stable light isotopic composition is reported in the delta notation as follows:

$$\delta\ (‰) = \left[\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 1000$$

where R is the heavy: light isotope ratio in the sample or standard respectively, e.g., $^{13}C/^{12}C$ or $^{18}O/^{16}O$ or $^{15}N/^{14}N$. The result is expressed as $\delta^{13}C$, $\delta^{18}O$ or $\delta^{15}N$ in the units ‰ (parts per thousand, or parts per mille).

$^{13}C/^{12}C$ ratios are presented relative to the Vienna PeeDee Belemnite (VPDB) standard.

$^{18}O/^{16}O$ ratios are presented relative to the Vienna PeeDee Belemnite (VPDB) standard.

$^{15}N/^{14}N$ ratios are presented relative to the Air standard.

2.4 Carbon

Carbon has two stable isotopes, ^{12}C and ^{13}C. Approximately 99% of carbon is ^{12}C and 1% is ^{13}C, with the contribution of additional isotopes being negligible. The carbon cycle moves CO_2 between the atmosphere and terrestrial and marine ecosystems (Peterson and Fry, 1987). Plants form the base of the food web and take up atmospheric CO_2 during photosynthesis. During this process, ^{12}C is favoured over ^{13}C; this discrimination occurs at both physical (e.g., diffusion) and enzymatic (uptake by photosynthetic enzymes) steps. As a result, plant tissues contain less ^{13}C and more ^{12}C than atmospheric carbon dioxide, with plant tissues having more negative $\delta^{13}C$ values. The level of discrimination varies according to the way in which plants photosynthesise (Farquhar *et al.*, 1988; Farquhar *et al.*, 1989; Brugnoli and Farquhar, 2000; Marshall *et al.*, 2007). Regardless of the photosynthetic pathway employed, fractionation associated with photosynthesis is the major determinant of $^{13}C/^{12}C$ ratios in an ecosystem. Animal tissues reflect the $\delta^{13}C$ of the plants they consume. It is for this reason that carbon isotopes have been used extensively for diet reconstructions in both contemporary and palaeo ecological studies. However in order to do this accurately one must understand the factors that cause variation in plant and animal $\delta^{13}C$.

[1] Defined as the "partitioning of isotopes between two substances or phases of the same substance with different isotope ratios" (Hoefs, 2004).

2.4.1 Carbon isotope variations in plants

The most significant source of $\delta^{13}C$ variation in plants is the fractionation that occurs during photosynthesis (Smith and Epstein, 1971). Environmental factors impact the efficiency of photosynthesis, causing further variations in $\delta^{13}C$. There may also be variation in $\delta^{13}C$ due to the source carbon dioxide which the plant uses for photosynthesis.

Dicotyledonous plants, such as trees, shrubs and temperate grasses, use the Calvin-Benson photosynthetic pathway. The first step in this process is the diffusion of CO_2 from the air into the stomata (pores in the epidermis of leaves) (Figure 2.4 illustrates the steps in the photosynthetic process.). The $^{12}CO_2$ molecule diffuses more readily than the heavier $^{13}CO_2$, so that the basic material for photosynthesis already comprises a greater proportion of ^{12}C than the atmosphere. The proportion of ^{12}C depends on whether the stomata are fully open or only partially open, which itself depends on environmental factors such as temperature and moisture availability or humidity.

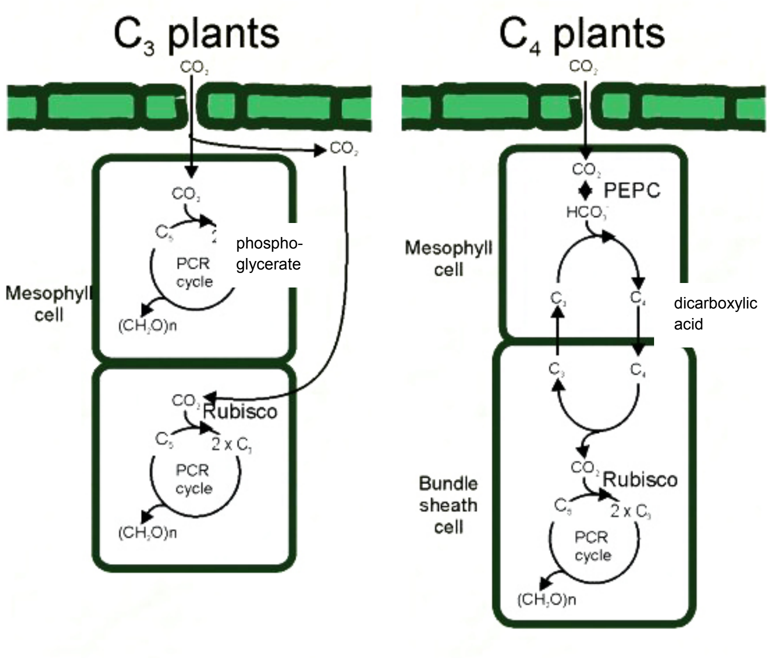

Figure 2. 4 Diagram illustrating the process of C_3 and C_4 photosynthesis (Adapted from (Lara and Andreo, 2011, Fig 1, p. 416)).

In C_3 plants, the enzyme rubisco catalyzes the photosynthesis and strongly favours ^{12}C over ^{13}C. This type of photosynthesis is called C_3 photosynthesis because the initial compound that is created is a 3-carbon molecule, phosphoglycerate (Figure 2.4). During this process, a CO_2 molecule is produced and then lost through the stomata during photorespiration. The loss of this molecule adversely affects the efficiency of this type of photosynthesis in terms of its ability to convert CO_2 into fixed carbon (Brugnoli and Farquhar, 2000; Adams, 2010).

The $\delta^{13}C$ of atmospheric CO_2 is currently about -8.4‰ (Keeling *et al*., 2009), a value that has been decreasing (and is continuing to do so) due to the input of ^{13}C-depleted CO_2 from fossil fuel burning (Freyer, 1986; Fry, 2006). Furthermore, as depicted in Figure 2.5, the net fractionation that occurs in C_3 photosynthesis is about 21‰, so that the average $\delta^{13}C$ value of all C_3 plants as measured in the 1980s and 1990s is -28 ± 2.3 ‰ (Peterson and Fry, 1987; Cerling *et al*., 1997).

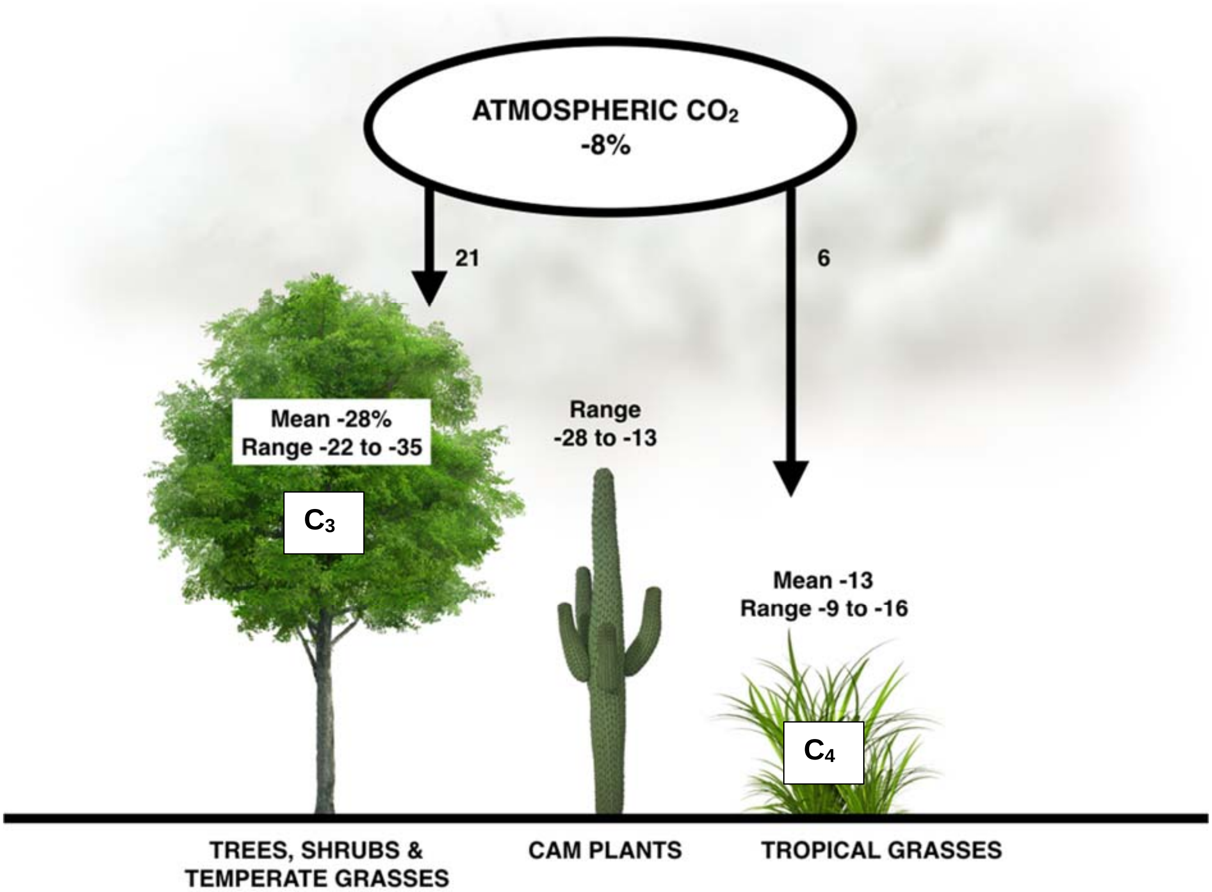

Figure 2. 5 Diagram illustrating the fractionation factors between atmospheric CO_2 and plant tissue with typical $\delta^{13}C$ values (in ‰).

In some plants (mainly tropical grasses), the phosphoenol pyruvate (PEP) carboxylase enzyme catalyzes the first stage of photosynthesis, resulting in the formation of a 4-carbon containing compound, dicarboxylic acid (Figure 2.4). This process is referred to as C_4 photosynthesis. This 4-carbon compound is then transported into the bundle sheaths of the leaf where the CO_2 that is released by the first step of photosynthesis (photorespiration) is reabsorbed and re-fixed by rubisco, resulting in no CO_2 being lost (Marshall *et al*., 2007) (Figure 2.4). As PEP carboxylase has a weaker preference for $^{12}CO_2$ than rubisco, and due to the fact that this type of photosynthesis "uses up" most of the CO_2 that is taken up, C_4 plant tissue contains more ^{13}C than C_3 plants. The average $\delta^{13}C$ for C_4 plants is around -12.5 ±1.1‰. Moreover, as depicted in Figure 2.5, the ranges for C_3 and C_4 plants are distinct and do not overlap. C_4 plants have several sub-types: NADP-ME, NAD-ME and PCK, named after the respective enzymes that catalyze the release of carbon dioxide from the carboxyl group (or decarboxylase acids) (Murphy and Bowman, 2009).

The third type of photosynthesis is CAM (Crassulacean Acid Metabolism) and is associated with succulent, fleshy leafed or stemmed plants which are adapted to arid conditions. These plants rely on the same enzymes as C_4 plants (indicated in Figure 2.4) but they separate the photosynthetic steps in terms of day and night. Specifically, these plants open their stomata to take up CO_2 at night when evaporation is low (Adams, 2010), thus avoiding water loss that would occur if they opened their stomata during the day (Smith *et al.* , 1976; West *et al*., 2006; Adams, 2010). At night, CO_2 is fixed by PEP carboxylase into C_4 acids which are stored in fleshy leaves or stems. During the day, acids are released and re-fixed by rubisco. If conditions favour C_3 photosynthesis, the $\delta^{13}C$ values of CAM plants can be indistinguishable from C_3 plants; they can also fall into the C_4 range or anywhere in between.

This range in $\delta^{13}C$ values is largely dependent on whether CAM plants can be flexible and photosynthesise both during the day and at night (non-obligate) (Segalen *et al.,* 2002). It is mostly the smaller, leafy succulents that can be flexible, depending on water availability (Mooney *et al.*, 1977). In the dry months, they mostly open their stomata at night, but in the wet season, they can shift to opening their stomata during the day (Mooney *et al.*, 1977). *Portulacaria afra* (Spekboom), commonly found in the Albany Thicket, is one of these succulents (Guralnick and Ting, 1987). Obligate CAM plants are mostly large-stem succulents (such as cacti), which open their stomata only at night regardless of water availability.

Environmental effects such as aridity also play a large role in determining plant $\delta^{13}C$. The $\delta^{13}C$ of C_3 plants is influenced by the ratio of intercellular to ambient concentrations of CO_2 (c_i/c_a) (Farquhar *et al.*, 1989), regulated by the degree of closure of the stomata (Figure 2.6). This is related to the water-use efficiency (WUE[2]) of the plant.

[2] WUE is defined as the ratio of net photosynthesis to transpiration (loss of water from the leaf) (Marshall *et al.* 2007).

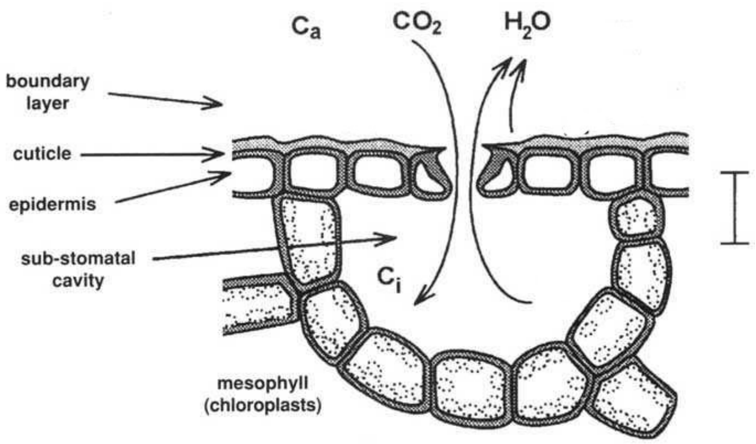

Figure 2. 6 Illustration of stomatal conductance from a leaf: the flow of CO_2 into the open stoma and H2O vapourising out of the stoma (Van de Geijn *et al.*, 1996, Fig 5.2, p. 105).

Both WUE and $\delta^{13}C$ in C_3 plants are controlled by intercellular CO_2 levels, making WUE and $\delta^{13}C$ of C_3 plant tissues closely related to each other (Farquhar *et al.*, 1982; Dawson *et al.*, 2002). During the process of stomatal closure due to water stress, the photosynthetic rates declines less than transpiration, increasing WUE. At the same time, the intercellular concentration of CO_2 is reduced and the $\delta^{13}C$ of fixed carbon becomes more positive. Therefore, C_3 plants in water-limited areas are enriched in ^{13}C.

Evidence of this is found in global patterns of foliar $\delta^{13}C$ of C_3 plant species from North America, Asia and Europe (Diefendorf *et al.*, 2010). The authors use a meta-analysis of published data to explore correlations in leaf $\delta^{13}C$ with various environmental parameters. For North America and Asian, mean annual precipitation was the strongest predictor of $\delta^{13}C$ in the leaves of C_3 plants. However, this was not the case in Europe, much of which is a winter rainfall zone. The suggestion is that patterns of water availability during the growing season might be the reason why this relationship is not observed in Europe (Diefendorf *et al.*, 2010). MAP does not always capture the subtleties of the seasonality of rainfall. Other measures for water availability such as amount of water in the growing season may be a better fit.

In their examination of water-stressed plants in Southern Africa, Swap *et al*. (2004) investigated the correlation between rainfall and $\delta^{13}C$ in C_3 and C_4 plants. A weak negative correlation (r^2 = 0.2) was identified for C_3 plants but no relationship was observed for C_4 plants. A study of both C_3 and C_4 Australian grasses (Murphy and Bowman, 2009) found a similar relationship between water availability and $\delta^{13}C$ of C_3 grasses (r^2 = 0.21). This study also found a low correlation with precipitation and $\delta^{13}C$ of C_4 plants. However when the different biochemical C_4 subtypes were accounted for, a stronger correlation was found (r^2 = 0.48) (Murphy and Bowman, 2009). Another Australian study found a strong correlation between $\delta^{13}C$ of C_3 plants and long term rainfall, number of rain days and a moisture availability index (calculated as rainfall minus evaporation) (r^2 = 0.78,0.70 and 0.74, respectively) (Stewart *et al.*, 1995). These correlation coefficients seem high compared with other studies, but it should be noted that Stewart *et al.* (1995) used mean $\delta^{13}C$ values per site. When individual observations were used, the r^2 value for rainfall dropped to 0.42.

Temperature is another important environmental variable that affects plant $\delta^{13}C$. At high temperatures, the enzyme rubisco is less efficient, leading to greater photorespiration. The yield of fixed carbon in C_3 plants thus decreases with increasing temperatures (Ehleringer *et al.*, 1997). Figure 2.7 shows that at any given CO_2 concentration, C_4 plants will be more efficient at higher temperatures (Ehleringer *et al.*, 1997). In addition, C_4 plants can fix more CO_2 than C_3 plants during times of low atmospheric CO_2, particularly at high temperatures (Ehleringer *et al.*, 1997; Adams, 2010). For this reason, C_3 grasses occur mainly in winter rainfall areas with cool growing seasons, and C_4 grasses occur in summer rainfall areas with warm growing seasons.

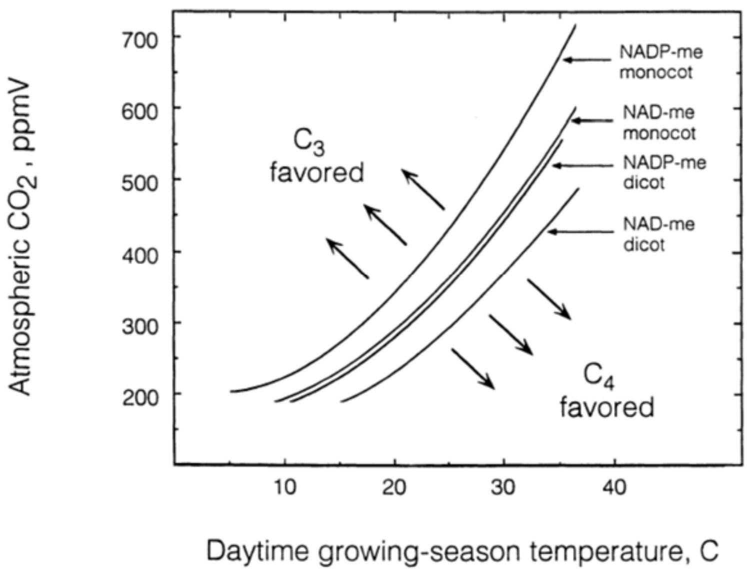

Figure 2. 7 Modelled crossover temperatures of the quantum yield for CO_2 uptake for C_3 and different sub-types of C_4 plants as a function of atmospheric CO_2 concentrations (Cerling *et al*., 1997, Figure 4, p. 157; Ehleringer *et al*., 1997, Figure 2, p. 292).

As with water availability, temperature also affects stomatal conductance. Murphy and Bowman (2009) examined the foliar $\delta^{13}C$ of Australian grasses in an attempt to correlate these to environmental variables such as temperature and water availability. They found significant relationships between $\delta^{13}C$ and water availability, but a less significant relationship between $\delta^{13}C$ and temperature.

CAM plants take up CO_2 at times of lower evaporative demand (usually at night) and are thus able to conserve water more effectively than C_3 photosynthesisers (Herrera, 2009). Non-obligate CAM plants can have a range of $\delta^{13}C$ in response to temperature due to daytime decarboxylation and higher transpiration (Herrera, 2009).

Variation in $\delta^{13}C$ of source CO_2 also causes variation in plant $\delta^{13}C$. In closed canopy forests, ^{13}C-depleted CO_2 respired by microbes is obstructed by the forest canopy from mixing with the atmosphere (Van Der Merwe and Medina, 1989; Van Der Merwe and Medina, 1991; Cerling *et al.*, 2004). This leads to more negative $\delta^{13}C$ values in plants on the forest floor. Different leaves from the same plant can show a gradient in $\delta^{13}C$ through the height of the canopy, with the lowest leaves demonstrating an enrichment in ^{12}C, while the highest leaves have better access to atmospheric CO_2 and have correspondingly more positive $\delta^{13}C$ values (Vogel, 1978a). In general, CO_2 available to plants in open systems, such as the savanna, should have $\delta^{13}C$ close to those of the atmosphere as a whole while the CO_2 available to plants within a closed canopy forest should be significantly lower (by as much as 2‰) and vary according to both the amount of soil-respired CO_2 and the extent of mixing with the atmosphere (Schoeninger, 2010).

Another source of variation in atmospheric $\delta^{13}C$ is historical. Due to fossil fuel combustion, the atmospheric concentration of CO_2 has increased over time while its $\delta^{13}C$ has decreased (Freyer, 1986; Vaughn *et al.*, 2010). The $\delta^{13}C$ of pre-industrial atmospheric CO_2 was approximately -6.5‰ (Friedli *et al.*, 1986; Indermühle *et al.,* 1999). This fact is important for studies that compare modern materials with ones that pre-date the industrial revolution.

The $\delta^{13}C$ values of plants can vary depending on the plant tissue being examined (O'Leary, 1981; Marshall *et al.*, 2007). In C_3 plants, there is evidence of ^{13}C enrichment in non-photosynthetic tissues compared with leaves (Cernusak *et al.,* 2009). Plant stems and roots are on average 1-2‰ more enriched than leaves (Badeck *et al.*, 2005) in part due to the range of chemical components that comprise various types of plant tissue (Marshall *et al.,* 2007). Intra-plant variations are not noted in C_4 plants, where no differences in $\delta^{13}C$ between roots and leaves have been observed (Cernusak *et al.*, 2009). This observation is important when considering browsers (which eat almost entirely C_3 plants) versus grazers (which eat C_3 and/or C_4 plants).

In summary, plant $\delta^{13}C$ varies mainly due to the type of photosynthetic pathway used. In addition, environmental variables influence the process of photosynthesis, leading to shifts in plant $\delta^{13}C$. These effects are more marked in C_3 plants, contributing to the wider range of $\delta^{13}C$ values in C_3 compared with C_4 plants.

2.4.2 Carbon isotope variations in animals

Carbon isotope ratios of foods are passed on to consumers with some additional fractionation (see insert box below) (Cerling and Harris, 1999; Hoefs, 2004; Passey *et al*., 2005; Codron *et al*., 2006a; Codron and Brink, 2007; Lee-Thorp, 2008; Codron *et al*., 2012b). The nature and extent of this additional fractionation is complex.

Fractionation/Discrimination Notation

Researchers express isotopic values and fractionation factors differently. Some works refer simply to enrichment (Hobson, 1999); some call it trophic level discrimination (Hedges and Reynard, 2007) while others discuss these factors in terms of diet-to-tissue spacing (Ambrose, 2002).

Capital Delta (Δ) is the difference between two delta values: $\Delta_{A-B} = \delta_A - \delta_B$

Epsilon (ε) takes into account the fact that delta values are ratios:

$$\varepsilon_{A-B} = \left[\frac{(\delta X_A + 1000)}{(\delta X_B + 1000)} - 1 \right] \times 1000$$

Epsilon values are, strictly speaking, more correct, but Δ values are more widely used in biological and ecological literature. In most cases, the difference between the two is very small.

In the present study, Δ will be used since the focus is on broad overall trends.

The most important influence on the $\delta^{13}C$ of animals is the $\delta^{13}C$ of the foods they consume, especially whether they are consuming C_3 or C_4 foods. Ungulates are usually described in terms of whether they consume grass (grazer), eat leaves of trees or shrubs (browser) or both (mixed feeder). Within these broad groups, animals with different feeding strategies (for example bulk feeders as opposed to selective feeders) may consume different parts of a plant, and might therefore be expected to have slightly different $\delta^{13}C$ values. Figure 2.8 illustrates the ranges observed for contemporary grazers, browser and mixed feeders from 27 bovid species from Southern Africa, mainly from summer rainfall areas.

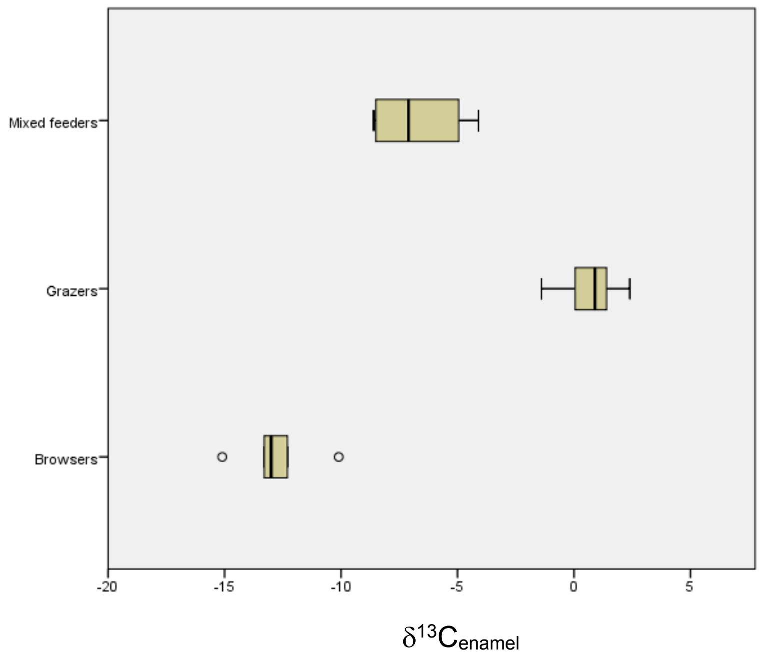

Figure 2. 8 Mean $\delta^{13}C$ values for bovids from Southern Africa indicating the range observed for grazers, browsers and mixed feeders (Data from Sponheimer *et al.* (2003a)).

The picture would look different in a winter rainfall area where C_3 grasses are present, where grazers would be expected to overlap with browsers. There have been a few isotopic studies in winter rainfall regions of South Africa, but they have been limited in their scope (Lee-Thorp *et al.*, 1989; Radloff, 2008). Radloff found that large grazers living in the Renosterveld portions of the Fynbos biome had much less negative $\delta^{13}C$ values than expected in a predominantly C_3 area (Radloff, 2008). Midgley and White (2016) measured the $\delta^{13}C$ of bontebok dung from De Hoop and found the average value to be -20.1 ± 2.4‰, reflecting approximately equal consumption of C_3 and C_4 grasses.

Carbon derived from dietary proteins, fats and carbohydrates is allocated differently in the synthesis of different tissues (referred to as routing) and thus not all body tissues reflect the same components of diet (Ambrose and Norr, 1993; Tieszen and Fagre, 1993; Codron *et al*., 2012b). Early feeding studies confirmed predictions that dietary amino acids are preferentially incorporated into protein tissues in the consumer, including bone collagen (Ambrose and Norr, 1993; Tieszen and Fagre, 1993). In fact, these authors believed that the carbon in bone collagen was derived entirely from dietary protein. However, the small animals used in these two studies were not good analogues for large bodied mammals since they differ in digestive physiology, metabolic rate, and feeding habits. Subsequent studies of pigs on controlled diets showed that $\delta^{13}C$ of non-essential amino acids in bone collagen correlated more closely with whole diet than with dietary protein (Howland *et al.*, 2003). In other words, dietary carbohydrates and lipids contribute to the carbon in non-essential amino acids in bone collagen. All dietary macronutrients contribute carbon to bone and enamel apatite.

There are different degrees of isotopic discrimination involved in the synthesis of different tissues (Tieszen and Fagre, 1993; Ambrose and Norr, 1993; Hobson *et al*., 2004; Codron *et al*., 2012b). Most body tissues are enriched in ^{13}C compared with diet, with the exception of lipids which are depleted in ^{13}C (DeNiro and Epstein, 1977). In large mammals, bone collagen is about 5.5‰ (see Figure 2.9) more enriched than diet (DeNiro and Epstein, 1978; Vogel, 1978b; Ambrose and DeNiro, 1986; Kellner and Schoeninger, 2007; Warinner and Tuross, 2009; Froehle *et al.*, 2010), while bioapatite (which is formed from blood bicarbonate) is 12-14‰ more enriched (Figure 2.9) (Lee-Thorp *et al.*, 1989; Cerling and Harris, 1999; Passey *et al*., 2005). Bioapatite in tooth enamel and bone are not isotopically equivalent, with more positive $\delta^{13}C$ values in enamel (Warinner and Tuross, 2009; Webb, White and Longstaffe, 2014). The cause of this is not fully understood, but the fact that tooth enamel is hydroxylated while bone apatite is not clearly indicates different synthetic processes (Webb *et al.*, 2014). Diet-to-enamel fractionation factors also vary according to species. Of particular relevance to this thesis is the fact that primates have a diet-to-enamel spacing approximately 1-2‰ smaller than the 14‰ observed in animals such as ungulates (Crowley, 2012; Sponheimer and Cerling, 2013; Schoeninger, 2014).

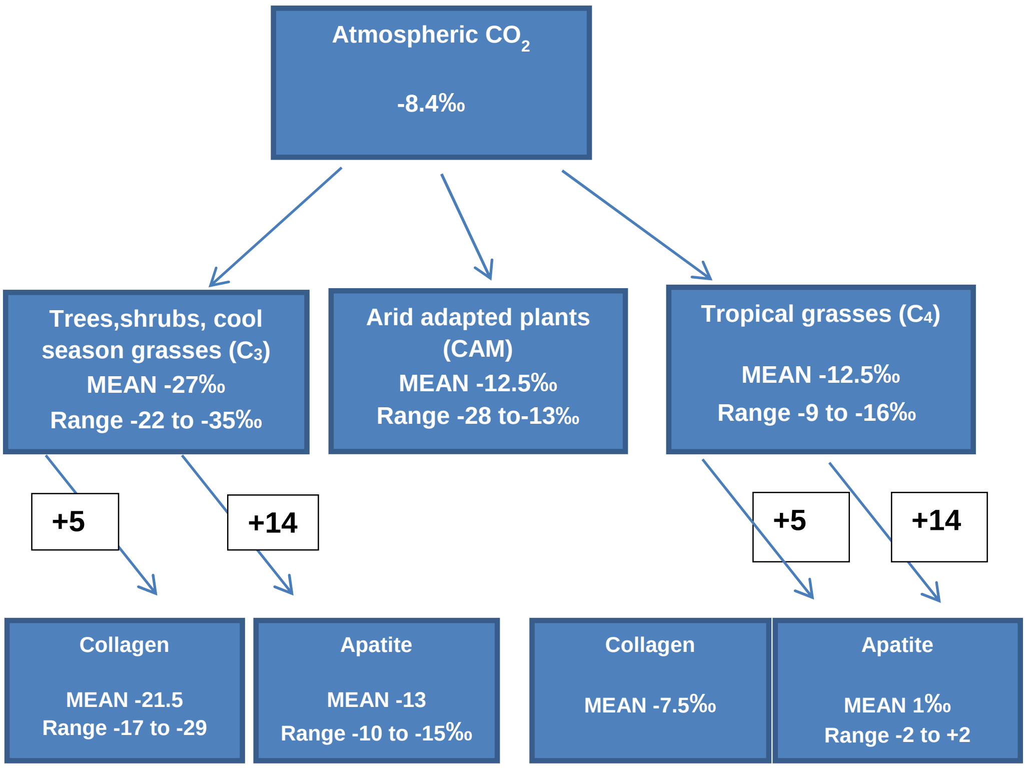

Figure 2. 9 Approximate fractionation factors for a terrestrial food web (Adapted from Lee-Thorp *et al.* (1989).

Diet-to-tissue discrimination factors vary by species, tissue, age, growth rate, digestive physiology and food quality (Caut *et al.*, 2009; Schoeninger, 2014). There are two ways of determining discrimination factors: controlled feeding experiments, where animal are kept in a confined space and fed a known diet, and the measurement of wild animals from natural habitats where the isotopic composition of the diet is already reasonably well characterised. Each scenario has advantages and disadvantages. Feeding experiments allow for better control over the isotopic composition of the diet. In order to keep the duration of the study within reasonable bounds, small, short-lived animals are more commonly used. Smaller animals may have very different metabolic processes when compared with large animals. Caut (2009) provides a useful review of discrimination factors based on feeding studies performed over a 25 year period. Those specifically dealing with bone collagen and enamel apatite include Ambrose and Norr (1993), Tieszen and Fagre (1993), Howland *et al.* (2003), Jim *et al.* (2004) and Warinner and Tuross (2009). It is difficult to accurately determine diet-to-tissue fractionation by field studies since the diet is not precisely known and because it is difficult to constantly monitor an animal's eating habits. Other factors that would alter diet-to-tissue fractionation include degree of activity (Schoeninger, 2014), whether the animal is growing or not, pregnancy and lactation. Digestive physiology also plays a role, and animals with simple digestive tracts such as humans have a smaller fractionation between diet and body tissue. Animals such as ungulates have a larger off-set between diet and enamel, for example, because of methane that is produced during microbial fermentation in the gut (Hedges and Van Klinken, 2002; Kellner and Schoeninger, 2007; Schoeninger, 2014)

Variations between $\delta^{13}C_{bone\ collagen}$ and $\delta^{13}C_{bone\ apatite}$ have also been studied (Krueger and Sullivan, 1984; Lee-Thorp *et al.*, 1989; Hedges, 2003; Jim *et al.*, 2004; Crowley, 2010; Crowley, 2012). However since the effects of diagenesis on bone apatite remain a concern (Lee-Thorp and Sponheimer, 2003), more studies have started comparing $\delta^{13}C_{bone\ collagen}$ and $\delta^{13}C_{enamel\ apatite}$ (Warinner and Tuross, 2009; Loftus and Sealy, 2012; Webb *et al.*, 2014) and reporting the offset between the two values ($\Delta_{apa\text{-}col}$). Early work found $\Delta_{apa\text{-}col}$ for herbivores to be about 7‰ while for carnivores, it was about 3‰ (Krueger and Sullivan, 1984; Lee-Thorp *et al.*, 1989). Omnivores lay in between with a $\Delta_{apa\text{-}col}$ of about 6‰ (Lee-Thorp *et al.*, 1989). This may be caused by differences in the amount of protein, lipids and carbohydrates in the diets of herbivores and carnivores (Hedges, 2003; Crowley, 2012) or differences in digestion, possibly with greater enrichment in herbivores that obtain nutrients from microbial fermentation in the gut (Hedges, 2003; Passey *et al*., 2005). Methane (CH_4) is produced during fermentation in the foregut (mainly in ruminants) or, to a lesser extent, in the hindgut. CH_4 is depleted in ^{13}C so when it is excreted from the body, it leaves behind a carbon pool more enriched in ^{13}C, leading to more positive $\delta^{13}C_{apatite}$ (Hedges, 2003; Koch, 2007).

Within the herbivore group, ruminants excrete more than double the amount of CH_4 (as a result of fermentation CH_4 is produced: $CH_3COOH \Rightarrow CH_4 + CO_2$) compared with hindgut-fermenting herbivores (Hedges, 2003), making the offset larger in ruminants. The mass of the animal also influences the amount of methane produced, with larger animals producing more methane (Smith *et al.*, 2010). However, variations in $\Delta_{apatite\text{-}collagen}$ are also noted in animals that do not produce significant amounts of methane, so methanogenesis alone is not sufficient explanation (Hedges, 2003). In carnivores, methanogenesis is almost negligible; they do not have the necessary methanogenic bacteria in their digestive tracts (Hackstein and van Alen, 1996). In kangaroos, $\Delta_{apatite\text{-}collagen}$ increases with aridity, which suggests that water availability may also be a factor (Murphy *et al.*, 2007). It remains unclear whether the smaller difference between collagen and apatite $\delta^{13}C$ in carnivores compared with herbivores is due to differences in the diet-to-collagen and/or diet-to-apatite enrichment.

Animals that eat only one type of food (stenotopic) show closer correlations between the isotopic values of their diet and body tissues (Codron *et al.*, 2011; Codron *et al.,* 2012b). In contrast, animals that eat a variety of foods, such as mixed feeders (e.g., springbok or goat) or some suids (e.g., warthog), exhibit some variation from this pattern (Codron *et al.*, 2011; Codron *et al.*, 2012b). The springbok, which switches comfortably between browsing in the dry season and grazing in the wet season, has an association between diet and body tissue that is not a 1:1 relationship (Codron *et al.*, 2012b). Goats fed a mixture of C_3 and C_4 plants (C_3 lucerne and C_4 grass) had an over-representation of the C_3 feed in their blood; this was interpreted as resulting from the higher protein content of lucerne compared with the C_4 grass (Codron *et al.,* 2011). Thus, it is clear that diet source heterogeneity plays a significant role in diet to tissue fractionation.

It was also hypothesised that since food sources differ in digestibility, the more digestible components of the diet would be represented in the body tissues while others would be excreted. When a change in diet was introduced for these goats, those that switched to C_4 grass incorporated the new $\delta^{13}C$ signal much more slowly than those initially on the C_3 lucerne diets. Furthermore, the isotopic value of the resulting body tissue never reached equilibrium (Codron *et al.*, 2011). Their and other studies (Ayliffe *et al.*, 2004) showed that the relationships between diet and body tissue are not simple, and variation in discrimination factors should not be underestimated.

Investigating $\delta^{13}C$ across environmental gradients has been of some interest due to its applicability to palaeostudies (Hoppe *et al.*, 2006; Fox-Dobbs *et al.*, 2007). Bump *et al.* (2007) set out to examine the validity of the idea that animals reflect in part the environment in which their food sources lived. The distribution of $\delta^{13}C$ across trophic levels was investigated. They found that the higher trophic levels best followed the changes in the environment. Thus they conclude that carnivores are good integrators of environmental signals, particularly the $\delta^{13}C$ of atmospheric CO_2 (Bump *et al*., 2007).

In palaeo studies, the C_3/C_4 distinction in carbon isotopes has been particularly useful in large-scale global environmental studies, such as the global expansion of C_4 grasses during the Miocene as recorded in fossil tooth enamel (Cerling *et al.,* 1997). Using the $\delta^{13}C_{enamel}$ of grazing species these authors showed that between about 8 and 6 mya there was a shift from a C_3 to a C_4 signal in Pakistan, East Africa, South America and North America. The pattern was not seen in Western Europe where cooler conditions and C_3 grasses prevailed.

In Southern Africa, C_4 plants expanded across areas that received at least some summer rainfall. Studies of ratite eggshell showed that this occurred in Namibia only in the last 3.5 million years (Segalen *et al*., 2002; Ségalen *et al.*, 2007; Ségalen and Lee-Thorp, 2009) (Fig. 2.10). However, C_4 grasses did not expand significantly into more temperate environments such as high-altitude grasslands and winter rainfall areas (Vogel *et al.,* 1978b; Mucina and Rutherford 2006).

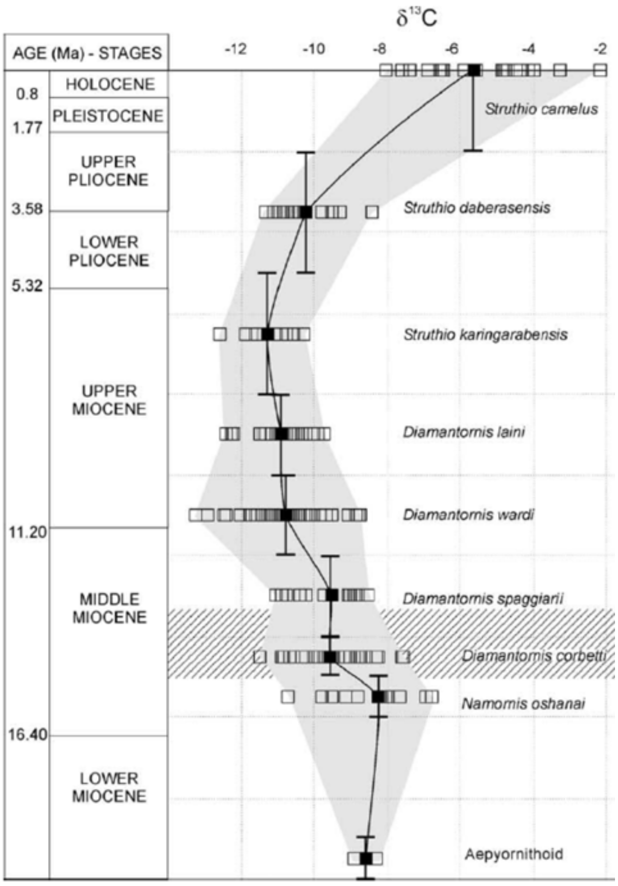

Figure 2. 10 Changes in ratite eggshell $\delta^{13}C$ over time from select sites in Namibia, Southern Africa (Segalen *et al*., 2002, Figure 2, p. 921).

At Langebaanweg, a Plio-Pleistocene site in the Western Cape dating to about 5 mya (Figure 2.11), Franz-Odendaal *et al.* (2002) measured the $\delta^{13}C_{enamel}$ of grazing fauna to investigate whether or not a winter rainfall regime existed in this region. They found a strong C_3 signal, indicating that C_4 grass expansion had not reached this region and that instead a winter rainfall regime characterised the area then as now (Franz-Odendaal *et al.*, 2002).

The presence of many large grazers dating to between 1-0.6 mya at the fossil site of Elandsfontein (Figure 2.11) in the Western Cape of South Africa has puzzled researchers for some time (Klein *et al.,* 2007). The contemporary vegetation in this area is Fynbos, which has a relatively small C_3 grass component (Vogel *et al.,* 1978; Bergh *et al.*, 2014). In the recent past, this environment did not support herds of large grazers. It was thus thought that the environment 1-0.6 mya must have been quite different, possibly including larger amounts of more palatable, possibly C_4 grasses. At that time, the area was a marsh frequented by fauna that came regularly to drink (Klein *et al.*, 2007). Rainfall would have been higher than today and may have extended into the summer months, supporting C_4 grasses. This hypothesis was tested by measuring $\delta^{13}C$ of grazers from Elandsfontein. Results showed no significant C_4 grass component, meaning that the vast majority of rain fell within the winter months (Luyt *et al.*, 2000; Lehmann *et al*., 2016). Large grazers may have travelled more widely, accessing a variety of food sources from further afield, or there may have been more C_3 grass than today (Owen-Smith and Danckwerts, 1997).

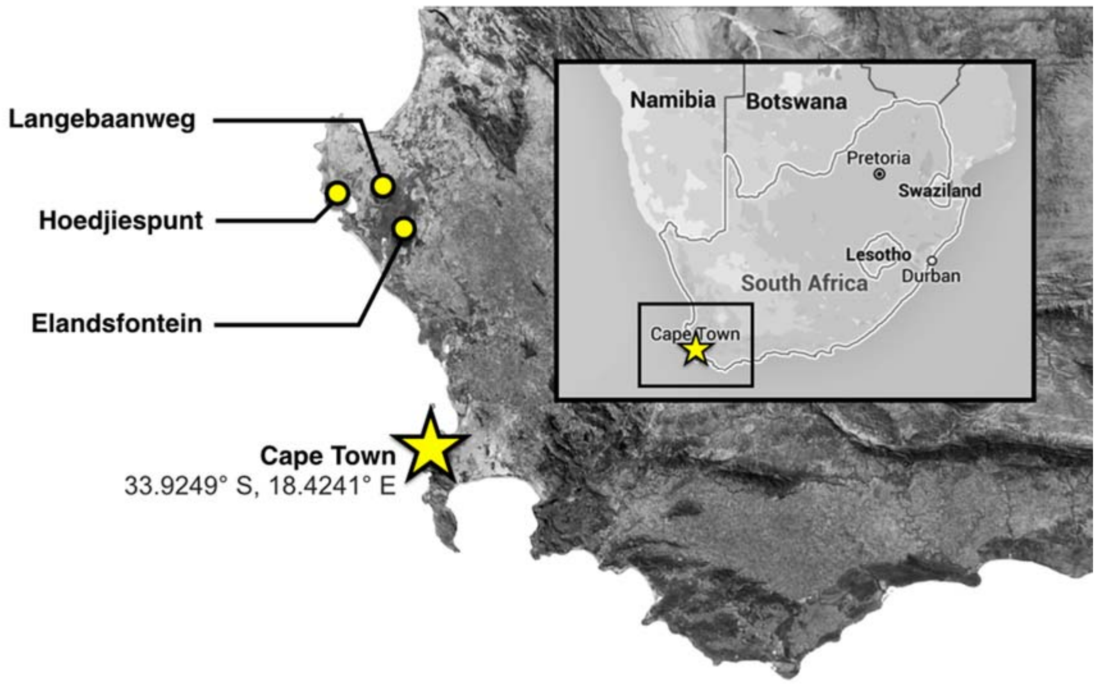

Figure 2. 11 Map indicating position of Elandsfontein, Hoedjiespunt and Langebaanweg (Map compiled by C. Louw).

Hoedjiespunt, which has yielded a few fragmentary remains of archaic *Homo sapiens*, is situated near Elandsfontein, also in the winter rainfall zone (Figure 2.11). Hoedjiespunt contains both an archaeological sequence (dated by infrared stimulated luminescence to between 40 kya and 240 kya) as well as older, underlying palaeontological material (for which the dating is much less resolved, but perhaps 200 kya to 300 kya) (Stynder *et al.,* 2001). $\delta^{13}C$ and $\delta^{18}O$ of faunal tooth enamel from the palaeontological layers at Hoedjiespunt found the vegetation to be predominantly C_3, although the values are slightly more enriched than those from Elandsfontein (Hare and Sealy, 2013). Since this isotopic shift was seen also in browsers, it cannot be explained by increased rainfall in the summer months. The authors suggest an inclusion of CAM plants in the diet or an environmental change, e.g., warmer and/or drier conditions. Interpretations of shifts such as this are, however, very difficult given our current state of knowledge. A better understanding of the complex relationships between environmental variables and stable isotope ratios in tooth enamel and bone collagen is needed to interpret data from archaeological and palaeontological sites such as these.

2.5 Oxygen

Oxygen is the most abundant element on earth. It is of great interest in biogeochemistry because it occurs in three phases: gas, liquid and solid. Oxygen has three stable isotopes: ^{18}O, ^{17}O and ^{16}O. Most oxygen atoms (99.8%) have 8 protons and 8 neutrons (^{16}O), but a small proportion (about 0.2%) contains 8 protons and 10 neutrons (^{18}O). An even smaller proportion (0.0375%) contains 8 protons and 9 neutrons (^{17}O); this isotope will not be discussed further in the present work.

Due to the strong link between climate and $\delta^{18}O$, oxygen isotopes have been studied in natural objects that record long periods of time, such as ice (Shackleton, 1987; Veres *et al*., 2013), speleothems (Talma and Vogel, 1992; Bar-Matthews *et al*., 2010) and, on a shorter time scale, tree-rings (Woodborne *et al.*, 2008; Hall *et al.*, 2008; Hall *et al.*, 2009; Brienen *et al*., 2012; Woodborne *et al*., 2015) and fauna (Sponheimer and Lee-Thorp, 1999a; Levin *et al*., 2006; Lee-Thorp and Sponheimer, 2007; Levin, 2008). $\delta^{18}O$ in animals depends mainly on ingested water from both food and drinking water.

2.5.1 Oxygen isotope variations in plants

There are three sources of variation in $\delta^{18}O$ for a plant: water, carbon dioxide and photorespiration (Sternberg, 1989). Oxygen in plant water has the greatest influence on the oxygen isotope ratio (Marshall *et al.*, 2007; McGuire and McDonnell, 2007; Barbour *et al.*, 2007). Plant water $\delta^{18}O$ depends on the $\delta^{18}O$ of the water source (Barbour *et al.*, 2007), the enrichment in ^{18}O that occurs during transpiration (DeNiro and Cooper, 1989; Barbour, 2007;

Barbour *et al.* , 2007) and the exchange between water and organic molecules during biosynthesis (Sternberg, 1989; Barbour *et al.*, 2007; Barbour, 2007).

$\delta^{18}O$ of precipitation (which accounts for most source water) is affected by a range of factors: the oceanic source from which it originates (van der Merwe, 2013), the amount of fractionation during evaporation, the fractionation that occurs while precipitation is developing and, finally, the trajectory of the associated air mass (McGuire and McDonnell, 2007). Of all possible influences, the temperature effect is most relevant to the present study as overall mean temperatures change in different environments. Seasonal variations in $\delta^{18}O_{pptation}$ cannot be identified in animal tissues such as bone due to the way bone forms and remodels. They can, however, be identified in tooth enamel through finely resolved serial sampling of individual teeth (Kohn *et al.*, 1998; Balasse *et al*., 2002).

$\delta^{18}O$ in precipitation is lower at higher latitudes (Marshall *et al.*, 2007) mainly because lower temperatures result in less $H_2{}^{18}O$ evaporating (McGuire and McDonnell, 2007). This trend is, however, only significant over quite large geographic regions. Within the plant, water is not isotopically fractionated when taken up nor when it is transported through the roots and stems. When it reaches the leaf and evaporation takes place, there is preferential loss of $H_2{}^{16}O$, leaving the leaves enriched in ^{18}O (Marshall *et al.*, 2007). The degree of isotopic enrichment of leaf water depends on:

- kinetic fractionation during diffusion from the stomata
- the pressure of water vapour
- isotope composition of the water vapour when compared with the source water and
- the ratio of ambient to intercellular water vapour pressure (Barbour *et al.* 2007).

Many of these variables are functions of the temperature and relative humidity of the environment. Thus, establishing the relative ^{18}O enrichment of the leaf versus the stem can predict relative humidity of the environment (Marshall 2007). As evaporation increases (at higher temperatures and in lower precipitation), leaves become more ^{18}O enriched (Barbour and Farquhar, 2000; Helliker and Ehleringer, 2000; Helliker and Ehleringer, 2002).

As illustrated in Figure 2.12, new plant growth happens at the base of the leaf where sucrose has been transported; the oldest part of the leaf is at the tip, and leaf water becomes increasingly enriched towards this portion of the leaf. Some base-to-tip differences in $\delta^{18}O$ are over 40‰ (Helliker and Ehleringer, 2002). The Péclet effect is the opposing effects of the convection of water towards the site of evaporation and the diffusion of the heavier isotope (^{18}O) away from the site of evaporation (Barbour *et al*., 2000; Helliker and Ehleringer, 2002; Barbour *et al*., 2004). In their study of variation in plant $\delta^{18}O$, Helliker and Ehleringer (2002) found that due to the length of the blade, the $\delta^{18}O$ of bulk leaf water of C_4 grasses was more enriched than those of C_3 dicot leaves. Moreover, the Péclet effect is amplified when transpiration is higher, which will make the leaf more enriched (Barbour *et al.,* 2004).

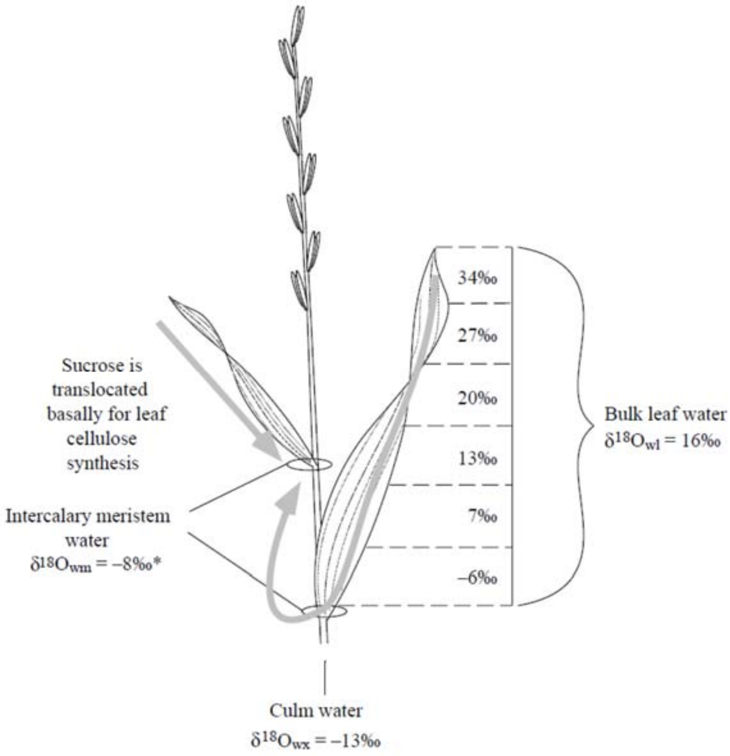

Figure 2. 12 Illustration of progressive leaf enrichment vs. overall bulk leaf (Helliker and Ehleringer, 2002, Figure 1, p. 436).

Oxygen isotopes are also fractionated during cellulose synthesis, with cellulose water being 27‰ more enriched in ^{18}O than stem water (Yakir and Deniro, 1990; Roden and Ehleringer, 2000).

In summary, it can be said that the $\delta^{18}O$ of plant tissues record important aspects of both a plant's growth environment as well as its particular physiological activity.

2.5.2 Oxygen isotope variations in animals

Since mammal bones and teeth are formed at a constant temperature that is unaffected by environmental temperature variations, the $\delta^{18}O$ of these tissues is directly related to $\delta^{18}O$ of the body water (Bryant and Froelich, 1995; Bryant *et al*., 1996; Lee-Thorp and Sponheimer, 2005; Lee-Thorp, 2008) (Figure 2.13).

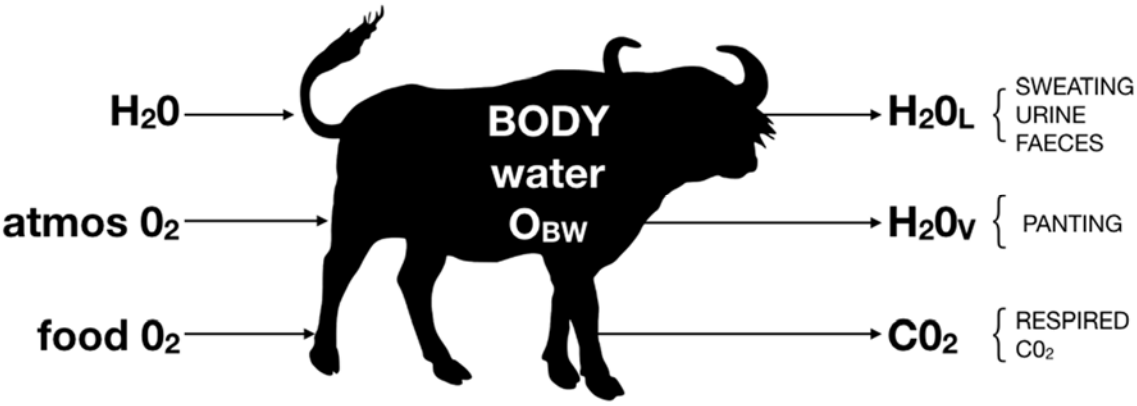

Figure 2. 13 Oxygen mass balance: inputs and outputs of oxygen into the body of mammals (Adapted from (Lee-Thorp, 2002, Figure 3, p. 441)).

Each of these inputs and outputs may be influenced by climate and/or physiological adaptations of the species, as well as the animal's diet (Ayliffe *et al.*, 1994; Bocherens *et al.*, 1996; Sponheimer and Lee-Thorp, 1999a; Hoppe, 2006; Murphy *et al.*, 2007). Inputs of oxygen into the body include drinking water, atmospheric O_2 and water in food. Outputs include urine, faeces, panting (water vapour), perspiration and respired CO_2. These dynamics are controlled by physiological processes and dietary and drinking behaviours. The isotopic composition of atmospheric oxygen is relatively constant and as such has a negligible effect on the $\delta^{18}O$ of fauna.

Mammals usually obtain their drinking water from meteoric[3] water (Koch, 2007). As outlined above, $\delta^{18}O$ of precipitation varies quite substantially. In certain regions in Australia, where source water has a relatively stable $\delta^{18}O$ value, the $\delta^{18}O$ of kangaroo bone phosphate has been found to be correlated with relative humidity (Ayliffe and Chivas, 1990). Kangaroos are not reliant on drinking water daily, instead obtaining most of their water from plant foods. Leaves would be expected to become more enriched in ^{18}O when relative humidity is lower (Ayliffe and Chivas, 1990).

In standing water, lighter molecules will evaporate first, leaving the remaining water relatively enriched. Oxygen isotope ratios from animals that obtain most of their water by drinking can thus provide clues to the degree of evaporation in their water source, which is related to temperature. This effect is not as pronounced in more extensive bodies of water as the larger volume of water mitigates enrichment (Koch, 2007).

[3] Meteoric water is water derived from precipitation (including lakes and rivers).

Helliker and Ehleringer (2000) demonstrated that because of the anatomy of the leaf (length in particular) and its water-use efficiency, $\delta^{18}O$ is more positive in C_4 than in C_3 grasses. However, this distinction becomes less evident in areas with high relative humidity. Evidence of this can be found in recent work at archaeological sites in South Africa. At both Elands Bay Cave (Stowe and Sealy, 2016) and Boomplaas (Sealy *et al.* in press), browsers were found to be more enriched in ^{18}O than grazers. Other South African sites where this pattern was not the case include Hoedjiespunt (Hare and Sealy, 2013) and Morea Estate (Sponheimer and Lee-Thorp, 2001), although in both these studies the sample numbers were low. Within the grazing subgroup, differences in $\delta^{18}O$ were noted at Equus Cave, where equids (bulk grazers that eat stems as well as leaves) were more depleted in ^{18}O than another type of grazer (*Antidorcas bondi*) that eats mainly new shoots (Sponheimer and Lee-Thorp, 1999a).

Oxygen outputs from mammals differ isotopically from body water depending on their phase. Liquid water, such as urine, sweat and faeces, all have an isotopic composition similar to body water (Wong *et al*., 1988; Bocherens *et al*., 1996; Sponheimer and Lee-Thorp, 2001). Water lost as vapour (from panting or respiration) is ^{18}O depleted relative to body water (Wong *et al*., 1988; Sponheimer and Lee-Thorp, 2001; Schoeninger *et al*., 2002). This pattern means that animals that sweat to reduce their body temperature should have lower $\delta^{18}O$ compared with animals that pant (Sponheimer and Lee-Thorp, 2001). These authors found that the waterbuck, which cools itself by sweating and panting, was more depleted in ^{18}O than herbivores that cool themselves primarily by panting.

While many studies centre on drinking behaviour and thermo-regulation (Kohn *et al.*, 1996; Kohn, 1996; Sponheimer and Lee-Thorp, 1999a; Lee-Thorp, 2008; Moritz *et al.*, 2012), patterns of carnivory can also be explored and established through $\delta^{18}O$. Carnivores such as hyenas had lower $\delta^{18}O$ values than herbivores (Lee-Thorp and Sponheimer, 2010). This may be because proteins are more depleted in ^{18}O than carbohydrates (Kohn, 1996). This observation is relevant when attempting to reconstruct hominin diets based on $\delta^{18}O$ of tooth enamel. It has also been suggested that the liquid water that carnivores obtain from prey is less enriched in ^{18}O than free water in most herbivore plant foods (Lee-Thorp and Sponheimer, 2010).

Body size affects the water mass balance in an animal (Schoeninger *et al.*, 2002). Body size is non-linearly related to the rates of oxygen fluxes through the body (Bryant and Froelich, 1995). Larger mammals (>1kg) have a constant body temperature which does not fluctuate with environmental temperature, while the temperatures of smaller mammals may fluctuate (Bryant and Froelich, 1995). In addition, there is a higher water flux in ruminants than non-ruminants of the same size, and liquid water influx and outflux increases with body size relative to other oxygen influxes and outfluxes (Bryant and Froelich, 1995). These authors also demonstrate that the fractionation of body water relative to source water decreases with increasing body size.

Using $\delta^{18}O$ of tooth enamel from faunal species across East Africa, Levin *et al.* (2006) developed a proxy for aridity. They classified each species as either evaporation sensitive (i.e., animals that ingest most of their water from plant material that would be affected by the level of evaporation) or evaporation insensitive (i.e., animals that obtain most of their water by drinking source water and would therefore not be affected by the level of evaporation). The authors found that evaporation insensitive animals tracked the $\delta^{18}O$ of the local water while the $\delta^{18}O$ of evaporation sensitive animals increased with aridity[4]. Furthermore, they found that the difference in oxygen isotope enrichment between the two groups reflected the degree of ^{18}O enrichment in plant water compared with source water. The more arid the environment, the bigger the difference in $\delta^{18}O$ between the two groups of animals.

This is an important proxy for aridity as it can be used for reconstructing palaeoclimates based on oxygen isotope analyses of fossil assemblages of fauna with known water preferences. As Levin *et al.*'s (2006) study was conducted in a summer rainfall area, it would be useful to test if the pattern applies in a winter rainfall region where the vast majority of plants, including grasses, are C_3. Such data could provide a means to speak more directly to aspects of water availability at archaeological sites at the time of their deposition.

2.6 Nitrogen

Nitrogen has two stable isotopes: ^{14}N and ^{15}N. ^{14}N comprises approximately 99.6% of all nitrogen and ^{15}N the remaining 0.4%. Atmospheric N_2 (which accounts for 99% of all nitrogen) has a $\delta^{15}N$ of 0‰ (Peterson and Fry, 1987). Atmospheric N_2 is fixed by microbes in the soil into ammonium, nitrite and nitrate. All of these can be inter-converted, with associated fractionation of nitrogen isotopes. These processes are complex, so $\delta^{15}N$ of soils will vary depending on what form the nitrogen is in and what processes of conversion have taken place. These conversions are in turn influenced by pH and moisture content (Ambrose, 1991; Koch, 2007; Szpak, 2014). Fixed nitrogen is lost via denitrification (the conversion of nitrate to N_2). This reaction fractionates nitrogen isotopes strongly, preferentially converting ^{14}N to N_2 gas

[4] Index used for aridity was "water deficit" in mm calculated as WD (water deficit) = PET (potential evapotranspiration) – MAP (mean annual precipitation). The authors used WD because relative humidity data was not available for their sites.

and leaving the soil enriched in ^{15}N. Soils with 'open' nitrogen cycles, in which extensive nitrogen fixation and denitrification occurs, therefore tend to have more positive $\delta^{15}N$ values.

2.6.1 Nitrogen isotopic variations in plants

Factors that contribute to the nitrogen isotopic composition at the level of the individual plant include: the form of nitrogen assimilated (atmospheric N_2, NH_4, NO_3), the mechanism of assimilation, where the nitrogen was assimilated (root or shoot) and where the nitrogen is then allocated (e.g., leaves, stem or fruit) (Szpak, 2014).

Some plants are nitrogen-fixers and have microbes in their rhizobia which can assimilate N_2 directly from the atmosphere. Such plants might be expected to have $\delta^{15}N$ values of around 0‰, close to that of the atmosphere (Peterson and Fry, 1987; Craine *et al*., 2009). In fact, the range is quite wide (between -10‰ and +10‰). Most plants, however, are unable to fix nitrogen themselves and instead assimilate ammonium (NH_4^+) or nitrate (NO_3^-) ions from the soil, which involves discriminating against ^{15}N. Nitrogen assimilation occurs primarily in leaves or roots with only a small amount occurring in the stem.

Mycorrhizal plants have different $\delta^{15}N$ compared with non-mycorrhizal plants (Chang and Handley, 2000; Spriggs and Dakora, 2009; Szpak, 2014). Mycorrhizal plants have a symbiotic relationship with fungal mycorrhizae, which have a large area of mycelium able to absorb nutrients (including nitrogen) from a larger volume of soil and provide them to the plant in exchange for photosynthetic products (Szpak, 2014). During the transfer of nitrogen-containing compounds, the mycorrhizae tend to retain the heavier isotope and thus mycorrhizal plants are more depleted in ^{15}N than non-mycorrhizal plants (Craine *et al*., 2009; Hobbie and Hogberg, 2012). For example, mycorrhizal plants (e.g., *Cyclopia*) growing in the Fynbos biome of South Africa have been shown to have $\delta^{15}N$ values between -3.6‰ and -0.1‰ (Spriggs and Dakora, 2009).

The soil depth at which nitrogen uptake occurs can also influence the $\delta^{15}N$ values of plants. Since soil $\delta^{15}N$ generally increases with depth, deeper-rooted plants usually have more positive $\delta^{15}N$ values (Amundson *et al*., 2003; Hobbie and Hogberg, 2012). This is true across various plant species, not just within a single species of plant (Hobbie and Hogberg, 2012).

A major influence on the ratio of $^{15}N/^{14}N$ in soils and plants is the availability of moisture, which depends on both precipitation and temperature (Heaton, 1987; Evans and Ehleringer, 1994; Koch, 2007). Wet ecosystems tend to conserve nitrogen, while dry ecosystems tend to lose nitrogen from the soil through denitrification, a loss which is large when compared with the size of the nitrogen pool (i.e., an open system) (Handley *et al*., 1999; Hedges *et al.*, 2004;

Szpak, 2014). In more mesic[5] environments, with more water availability but often less nitrogen, the nitrogen is recycled (i.e., less loss of nitrogen in a closed system) (Handley *et al*., 1999; Szpak, 2014). In other words, soils and plants in arid environments are enriched in ^{15}N due to the loss of nitrogen from such systems (Hedges *et al.*, 2004; Koch, 2007).

On a global scale, foliar δ^{15}N correlates negatively with rainfall (Handley *et al.*, 1999; Craine *et al.*, 2009). Murphy and Bowman (2009) investigated the response of C_3 and C_4 plants to climatic variables by examining δ^{15}N in Australian grasses and found a negative relationship between water availability and δ^{15}N (r^2=0.40) for both C_3 and C_4 plants. When they separated out the various types of C_4 plants, they found large differences in δ^{15}N for the various biochemical C_4 sub-types (differences of up to 5.1‰ were observed). (Murphy and Bowman, 2009). This result is somewhat different from that of Swap *et al.* (2004), whose study in Southern Africa showed a much stronger correlation between rainfall and δ^{15}N of C_3 plants (r^2=0.54) compared with C_4 plants (r^2=0.04). Murphy and Bowman (2009) concluded that it was water availability that controlled δ^{15}N. A South African study done in the Kruger National Park, where the rainfall varies from 300mm to 700mm per annum, found that neither C_4 grasses nor C_3 foliage were correlated with rainfall or temperature (r^2 ranging from 0.01 to 0.08). The authors postulate that this is due to the rainfall gradient in the park spanning such a small portion of the global range (Codron *et al.*, 2013).

In summary, the N isotopic biogeochemistry of plant-soil systems is complex with many environmental variables that can influence the nitrogen isotopic composition of plants. It seems that the "open-ness" or "closed-ness" of the nitrogen cycle (which is influenced by climate) is what controls the spatial variation of ^{15}N levels. Environments with higher water availability and lower temperatures tend to be characterised by less positive δ^{15}N values.

2.6.2 Nitrogen isotope variations in animals

The δ^{15}N in animal tissues reflects the types of food the animal consumes. Animal tissues are consistently enriched in ^{15}N compared with the food source (Schoeninger *et al.*, 1983; Schoeninger and DeNiro, 1984; Ambrose, 1991; Thackeray, 1996; Sponheimer *et al*., 2003b; Bocherens and Drucker, 2003; Codron *et al*., 2007a; Caut *et al.*, 2008; Caut *et al.*, 2009; Szpak *et al*., 2012; O'Connell *et al*., 2012). Stepwise enrichment/fractionation with trophic level[6] (referred to as trophic level enrichment*)* means that a herbivore will be more enriched in ^{15}N than the plants it consumes, and a carnivore will be more enriched than the herbivores it consumes (Figure 2.14). Thus, the ^{15}N/^{14}N ratio is a good indicator of trophic level and diet. It

[5] An environment containing a moderate amount of moisture.
[6] The trophic level of an organism is the position it occupies in a food chain. A food chain represents a succession of organisms that eat other organisms and are, in turn, eaten themselves.

should be remembered that nitrogen in animals is supplied almost entirely by dietary protein (Koch, 2007), which is different from carbon and oxygen that are supplied by all major categories of nutrients (proteins, lipids and carbohydrates). $\delta^{15}N$ values therefore track the protein component of the diet, not the whole diet.

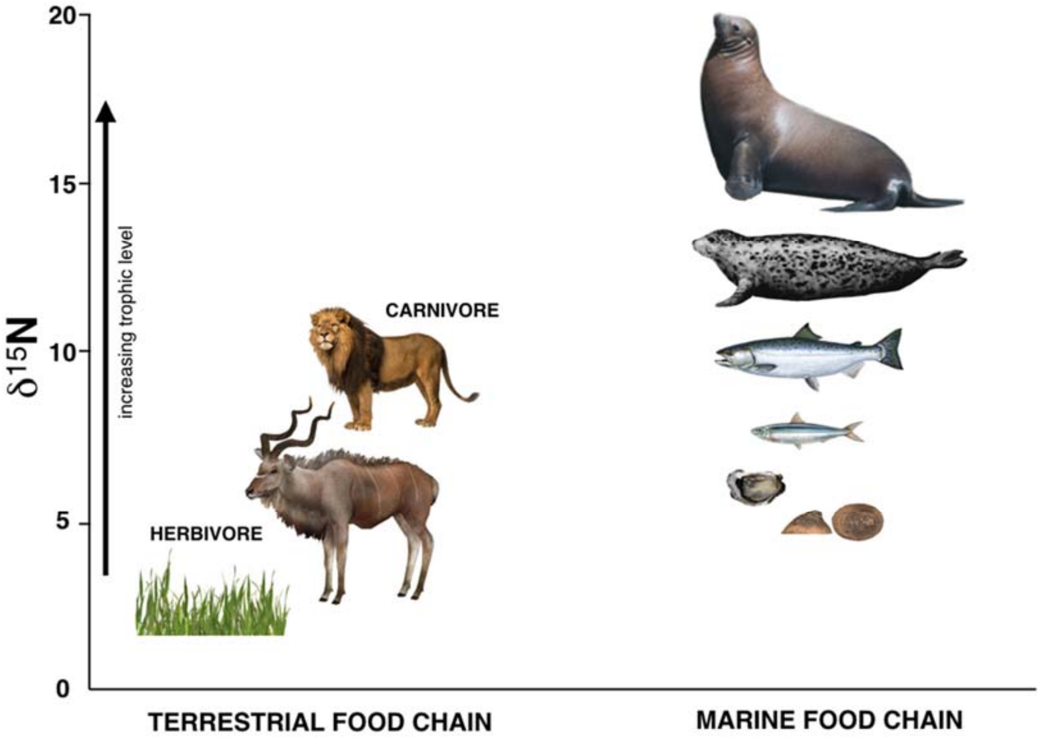

Figure 2. 14 $\delta^{15}N$ values of a terrestrial and a marine food chain showing a pattern of step-wise enrichment (Adapted from Schulting, 1998, Figure 2, p. 205).

The extent of the fractionation that occurs at each trophic level is debated. Enrichment varies across species and ranges substantially. Early studies (DeNiro and Epstein, 1981; Schoeninger *et al.*, 1983) proposed an enrichment of about 3-4‰, but some subsequent studies have proposed significantly larger values of up to 6‰ (O'Connell *et al*., 2012; Drucker and Bocherens, 2004). Fractionation factors differ in different body tissues. There are a multitude of studies investigating $\delta^{15}N$ in the hair and faeces of ungulates (Sponheimer *et al.,* 2003b; Sponheimer *et al*., 2003c; Codron *et al*., 2006b; Codron *et al.,* 2007a; Codron *et al*., 2007b; Codron *et al.*, 2012a; Codron *et al.*, 2012b; Clauss *et al.*, 2014). Fractionation values for muscle, feather, plasma, liver, blood have been collected in meta–data analyses (Kelly, 2000; Vanderklift and Ponsard, 2003; Caut, Angulo and Courchamp, 2009). Caut *et al.* (2009) also report a handful of collagen fractionation factors, but only for birds. As this study focuses on isotope ratios in bones and teeth, the focus of this section with be on $\delta^{15}N$ in bone collagen.

Variation in bone $\delta^{15}N$ in animals may be influenced by the following factors:

1. isotope values of source nitrogen in the diet (which in turn is influenced by climate);
2. environmental stress (aridity or lack of food);
3. digestive physiology;
4. the amount and quality of protein in the diet.

The most important determinant of $\delta^{15}N$ in animals is the nitrogen isotope composition of the foods they consume, whether it be plants or animals. Variations in plant $\delta^{15}N$ along aridity gradients at scales ranging from the local to the continental are passed on to consumers (Gröcke *et al.*, 1997; Schulze *et al.*, 1998; Schwarcz *et al.*, 1999; Iacumin *et al.*, 2000; Kelly, 2000; Richards and Hedges, 2003; Hedges *et al.*, 2004; Stevens and Hedges, 2004; Murphy and Bowman, 2006; Smiley *et al.*, 2015). In a widely cited study, Murphy and Bowman (2006) showed that variation in kangaroo $\delta^{15}N_{collagen}$ across environmental gradients in Australia parallels variation in plant $\delta^{15}N$. Both kangaroos and plants yielded more elevated $\delta^{15}N$ in arid environments, but the offset between foliar and bone collagen $\delta^{15}N$ remained approximately constant, indicating that the patterns seen in kangaroos were driven by those in the plants (Murphy and Bowman, 2006).

Kelly *et al.* (2000) compiled $\delta^{15}N_{collagen}$ data from 60 studies of mammals worldwide. Their meta-data confirmed that elevated $\delta^{15}N$ is found at dry locations; herbivores from mesic environments have mean $\delta^{15}N_{collagen}$ of 6.3 ± 2.2‰ (n=23) and those from xeric environments have a mean of 8.7 ± 2.8‰ (n=12). However, a recent study from North America shows that the dietary $\delta^{15}N_{hair}$ signal from two species of rodent are not well correlated with environmental factors when compared with the correlations found for $\delta^{13}C$ (Smiley *et al.,* 2015). Furthermore, those correlations that were significant were mostly negative, implying that water availability is controlling the $\delta^{15}N_{hair}$ in these species to some degree.

A number of studies have suggested that metabolic processes within animals also contribute to elevated $\delta^{15}N$ in arid environments. In an early paper, Schoeninger and DeNiro (1984) reported high $\delta^{15}N$ values for drought-tolerant animals such as kangaroos. They suggested that the amino acid synthesis in drought tolerant animals is different from other animals, causing elevated $\delta^{15}N$. Ambrose (1991) suggested that this is because the urea being excreted is more ^{15}N depleted in drought-stressed animals (i.e., a concentration of urea), leaving body tissues enriched in ^{15}N (Ambrose and DeNiro, 1986; Ambrose, 1991; Ambrose, 1993). On the other hand, animals in arid regions may increase the recycling of urea within their bodies in an effort to conserve nitrogen (Sealy *et al.,* 1987). However, Ambrose (1991) indicates that due to nitrogen mass balance, unless animals actually excrete ^{15}N depleted nitrogen, the animal's body tissues will not become enriched in ^{15}N. It may therefore be expected that drought-tolerant animals (or water independent animals) should have higher $\delta^{15}N$ values than obligate drinkers (or water dependent animals). Evidence for this is reported by Ambrose and DeNiro (1986) where obligate drinkers have a lower $\delta^{15}N_{collagen}$ mean than drought resistant animals.

Subsequent studies have found similar patterns (Sealy *et al*., 1987; Gröcke, Bocherens and Mariotti, 1997; Schwarcz *et al.*, 1999; Pate and Anson, 2008). Two early studies reported $\delta^{15}N$ values of fauna in the winter rainfall area of South Africa (Heaton *et al.,* 1986; Sealy *et al.* 1987). Both showed that animals from arid environments have more positive $\delta^{15}N_{collagen}$ values (Figure 2.15 is a compilation of the four studies that measured $\delta^{15}N_{collagen}$ against MAP). Using the model proposed by Ambrose and DeNiro (1986), Sealy *et al.* (1987) noted that herbivores that are obligate drinkers have lower $\delta^{15}N$ values than animals that are drought tolerant, and grazers have lower $\delta^{15}N$ values when compared to browsers. They also predicted, but could not prove using available datasets, that these differences would be more marked in arid environments (Sealy *et al.*, 1987). Murphy and Bowman (2006) disputed the influence of metabolic processes within animals, explaining variations in kangaroo $\delta^{15}N$ in terms of food eaten. However, kangaroos are a homogeneous group. Consideration of groups of animals with different digestive systems may yield more complexity.

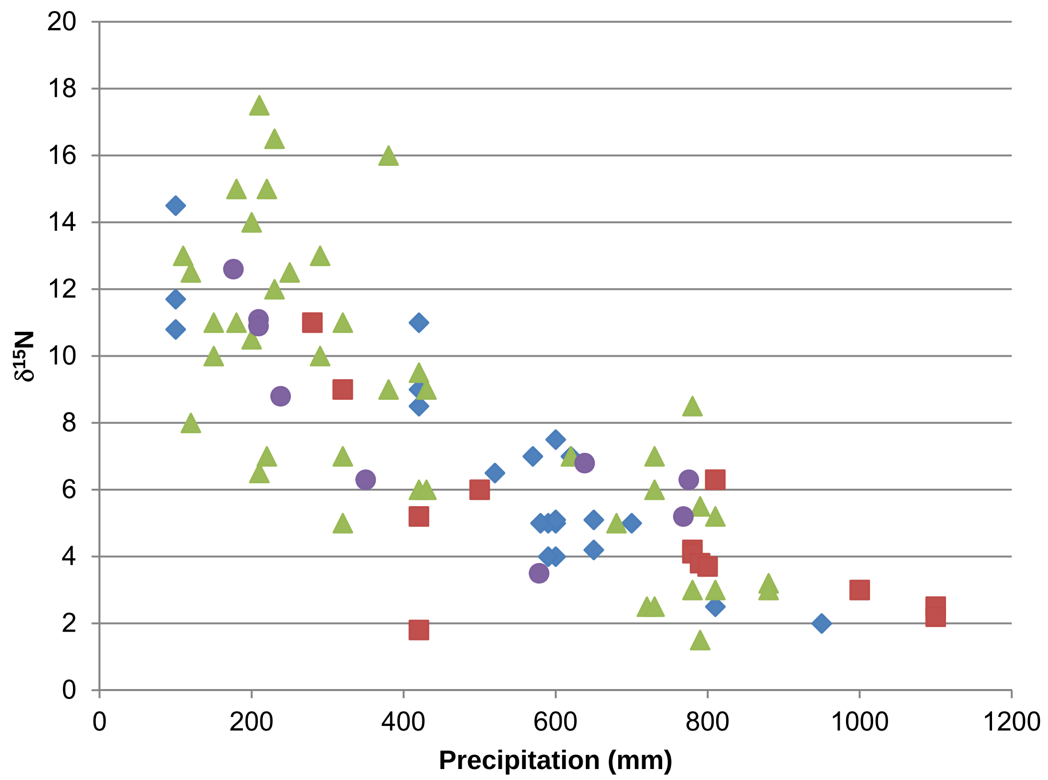

Figure 2. 15 Relationship between rainfall and faunal $\delta^{15}N_{collagen}$ from range of studies: Data compiled and extracted taken from Heaton *et al*. (1986)(blue diamonds) and Sealy *et al*. (1987) (green triangles) are for individual animals from Southern Africa; those from Cormie and Schwarcz (1996) (red squares) are individual deer consuming >10% C_4 from North America; Pate and Anson (2008) (purple circles) presented mean values for kangaroos (Macropus spp.) for South Australian collection sites.

Since it is the preferential excretion of ^{14}N that is thought to cause ^{15}N enrichment in mammals higher up in the food chain, Sponheimer *et al.* (2003b) set out to test this with a controlled feeding study on llamas. They pointed out that nitrogen is excreted in faeces as well as urine and that both should be considered in studies of ^{15}N enrichment in consumers. They showed that for llamas, no enrichment of faeces occurs with a change in protein in the diet and thus the amount of ^{15}N lost through faeces would have less of an effect on the relative enrichment of consumer tissues. In contrast, the urinary $\delta^{15}N$ was lower for animals on the low protein diet compared with the high protein diet, indicating that the amount of urine lost for llamas would influence the $\delta^{15}N$ of consumer tissues (Sponheimer *et al*., 2003b).

Pate and Anson (2008) correlated $\delta^{15}N$ in bone collagen from kangaroos with both relative humidity and rainfall (also in Figure 2.15). They found that below an average rainfall of 238 mm, a positive correlation exists between mean annual rainfall and kangaroo $\delta^{15}N$ (r^2=0.98) but above this threshold the correlation is non-existent (r^2=0.0011) (Pate and Anson, 2008). In Kenya, Cerling *et al.,* (2009) reported increased $\delta^{15}N$ in elephant tail hair after rainfall. This was part of a pattern of rapid growth of grass after rainfall, shifting the elephants' carbon as well as nitrogen isotope ratios. Since Kenya is a summer rainfall zone, it is not clear whether the same pattern would hold in the winter rainfall area.

Considering palaeo datasets, a marked decrease in $\delta^{15}N_{collagen}$ was found for a range of animal species from Northern Europe and Western Asia shortly after the last glacial maximum (Hedges *et al.* , 2004). This was likely due to greater moisture availability, a condition that may have resulted from melting ice-sheets and perhaps also increased precipitation. This would have altered the nitrogen cycle in the soil (Iacumin *et al.*, 2000; Hedges *et al.*, 2004).

Gröcke *et al.* (1997) used the pattern of variation in modern kangaroo $\delta^{15}N$ along with rainfall records to retrodict past precipitation using ancient kangaroo $\delta^{15}N$. They found a strong negative relationship between kangaroo $\delta^{15}N_{collagen}$ and water availability. However, a subsequent study by Murphy and Bowman (2006) suggested that the modern sample used by Gröcke *et al.* (1997) was too small to capture the range of variation adequately.

Nutritional stress plays a role in the fractionation of nitrogen isotopes during tissue synthesis (Hobson *et al.*, 1993; Kelly, 2000; Adams and Sterner, 2000; Oelbermann and Scheu, 2002; Robbins *et al.*, 2005; Fuller *et al.*, 2005; Kuitems *et al.*, 2015). During times of nutritional stress when the body catabolises its own tissues, $\delta^{15}N$ values become more positive (Robbins *et al.*, 2005; Parker *et al.*, 2005). This is because during such times, there is inadequate nitrogen intake, but the loss of nitrogen continues (Adams and Sterner, 2000). Evidence for this in humans (and by extension, other mammals) comes from a study in which the hair of pregnant women (with nausea and weight loss) was measured to investigate the changes in $\delta^{15}N$ (Fuller *et al.*, 2005). They found that $\delta^{15}N$ values were elevated during pregnancy, while the women were drawing on their own body tissues for the foetus, and returned to previous levels once the baby had been delivered. Similar patterns have been reported for animals on low-protein diets (Hobson, 1999; Vanderklift and Ponsard, 2003; Voigt and Matt, 2004; Miron *et al.*, 2006).

These effects are, however, difficult to quantify in controlled feeding studies. Ambrose (2002) raised rats on diets that included varying amounts of protein in order to measure the effect on $\delta^{15}N_{collagen}$; he found no significant differences in $\delta^{15}N$ with the different levels of protein. Rats in this study were also subjected to water and heat stress, with no significant differences resulting in either of those groups (Ambrose, 2002). Robbins *et al.* (2005) set out to test whether ^{15}N discrimination in mammals increased with the level of protein in the diet, postulating that discrimination should increase with trophic level since carnivores ingest more protein than herbivores. Their meta-analysis of discrimination factors for serum, plasma and blood found that the level of discrimination was in fact the same or lower in carnivores compared with herbivores (Robbins *et al.*, 2005).

The nutritional quality of foods has also been investigated among herbivores (Codron *et al*., 2007b; Robbins *et al.*, 2010). Grasses, although easy to digest, are considered low quality feed, particularly in the dry season. Trees and shrubs are usually high in protein year-round and are therefore considered high quality feed (but more difficult to digest due to the presence of tannins and other secondary chemicals) (Codron *et al*., 2007b; Robbins *et al.*, 2010). Grasses also tend to be shallow-rooted compared with bushes and trees, so they may have lower $\delta^{15}N$ to start with (Evans and Ehleringer, 1993). Therefore grazers would be less likely to maintain their nitrogen mass balance during the dry season when compared with browsers (Sealy *et al.*, 1987; Ambrose, 1991).

The digestive physiology of the animal has also been suggested as an influence on animal $\delta^{15}N$. All herbivores have symbiotic cellulose-digesting bacteria within their guts. In animals with simple stomach structures, such as equids and rhinoceroses, fermentation assisted by bacteria occurs in the hindgut (Langer, 1984; Langer, 2002). In ruminants, which have four-compartment stomachs (Hofmann, 1989), bacterially assisted fermentation takes place in the foregut. Ruminants include grazers (such as gemsbok, red hartebeest and blue wildebeest) and browsers (such as grysbok, duiker, eland and kudu). It has been suggested that the digestion and absorption of microbes by ruminants adds an additional trophic level to the system (Sealy *et al*., 1987; Ambrose, 1991). Thus, some researchers might expect ruminants to have higher $\delta^{15}N$ values than non-ruminants (Sealy *et al*., 1987). Conversely, the location of microflora in hindgut fermenters means that the microfloral component would not be digested, as in the case of ruminants, and would actually be lost in the process of excreting faeces (Codron and Codron, 2009).

Few studies have had sufficiently large samples to investigate possible differences between $\delta^{15}N_{bone\ collagen}$ in ruminants and non-ruminants. A study in the Kruger National Park found that ruminant faeces had higher $\delta^{15}N$ values (mean = 5.17±1.5‰, n=1486) than non-ruminants (mean = 4.45±1.3‰, n=267) (Codron and Codron, 2009). Since the non-ruminants in this sample were all grazers, the authors compared ruminant and non-ruminant grazers and found that the difference persisted. Since the difference was less than 1‰, these authors concluded that eco-physiological adaptation was only a small part of this difference and that dietary protein content exerted the biggest influence on faecal $\delta^{15}N$ (Codron and Codron, 2009).

2.7 Summary: Carbon, Oxygen and Nitrogen Isotopes

Although body tissues such as bone collagen and tooth enamel reflect an individual's diet, their isotopic values can be expected to differ due to the timing of formation, turnover rates and fractionation during synthesis. Different teeth are reflective of different time periods and, as such, can form an account of that individual's life.

The patterning in stable carbon isotopes can be summarised as follows: there are two major photosynthetic pathways (C_3 and C_4) together with CAM. In regions with warm temperatures in the growing season, almost all the grasses follow the C_4 pathway, while trees, shrubs and herbs follow the C_3 pathway. This is the case in the African savanna regions where the rainy season is in summer. In temperate regions where the growing season is cool, the vast majority of plants, including grasses, follow the C_3 pathway. The CAM pathway is restricted mostly to succulent-type plants that, in South Africa, have limited distributions mostly towards the south and west coasts. The different photosynthesic pathways lead to distinct carbon isotopic ratios in C_3, C_4 and CAM plants. These are passed on to consumers and are reflected in the tissues of mammals. It is therefore possible to measure the isotopic composition of animals and calculate the proportion of C_3 or C_4 plants they consumed, which can be used to make inferences about past environments. The carbon isotope ratios of plants (especially C_3 plants) have been shown to vary with environmental factors such as moisture availability, as determined by precipitation and temperature (Swap *et al.*, 2004; Diefendorf *et al.*, 2010). The extent of these variations and the degree to which they are captured by consumer tissues requires closer investigation in order to interpret archaeological and palaeoecological datasets. Specifically, we would like to be able to quantify the type and magnitude of environmental change required to produce a specified shift in $\delta^{13}C$ of fossil or archaeological animal remains.

Oxygen isotope ratios in the carbonate and phosphate of calcified tissues, including enamel, are directly related to the isotopic composition and rates of flux of oxygen that enters and leaves an animal. $\delta^{18}O$ of different faunal species in the same ecosystem is likely to be explained by the differences in isotopic composition of the oxygen in food and liquid water and the way the animal regulates its temperature. It is thought that animals consuming evaporatively enriched leaves will have more positive $\delta^{18}O$ values relative to those getting their water from drinking water. Whether the $\delta^{18}O$ “aridity index” can also be used in the winter rainfall zone requires testing. Water-related behaviour and thermo-physiology in fossil fauna can be researched through the analysis of $\delta^{18}O$.

$\delta^{15}N$ patterning in fauna is complex. Values vary due to the nitrogen isotopic composition of the diet and the factors that affect the nitrogen mass balance in the animal. Both the $\delta^{15}N$ of the diet and the metabolic processes that occur within the animal after consumption are likely to respond to climate. It is currently understood that $\delta^{15}N$ in fauna pattern in the following ways. More positive $\delta^{15}N$ values are seen in animals from arid environments due partly to the elevated $\delta^{15}N$ in plants but also, to an unknown extent, to metabolic processes within the animals. More positive $\delta^{15}N$ values can probably also be seen in animals on diets that provide inadequate protein, in grazers compared with browsers, or in ruminants compared with non-ruminants. Animals at higher trophic levels have more positive $\delta^{15}N$. The studies reviewed above indicate that it is possible to use $\delta^{15}N$ values as indicators of past environmental changes but that patterning needs to be more extensively explored in the South African context before undertaking palaeo studies in this part of the world.

Chapter 3: Study region

3.1 Introduction

This study focuses on the winter rainfall zone in the extreme southwestern part of Africa. Chapter 3 provides an overview of the environmental and climatic conditions that characterise this region.

3.2 Study areas

3.2.1 Introduction

The geographic coverage of this study includes the west coast of South Africa from southern Namibia to Cape Town and the south coast from Cape Town to the Addo Elephant National Park. The northernmost part of this study area in the Kgalagadi National Park is not, strictly speaking, in the winter rainfall zone, but was included for comparative purposes. Figure 3.1 shows the contemporary extent of the winter and year-round rainfall zones in the study area. Southwestern South Africa has a number of reserves protected by South African National Parks (SanParks) or the provincial nature conservation body Western Cape Nature Conservation Board (Cape Nature). This makes it possible to collect samples of modern animals from relatively undisturbed natural environments in which they feed on indigenous vegetation. Modern communities of large mammals do not include all the species that were present in the past, but in most cases, the species that occur today were also present in the past, particularly during the late Holocene. These nature reserves occur in winter and year-round rainfall zones which exhibit varying levels of precipitation, relative humidity and temperature.

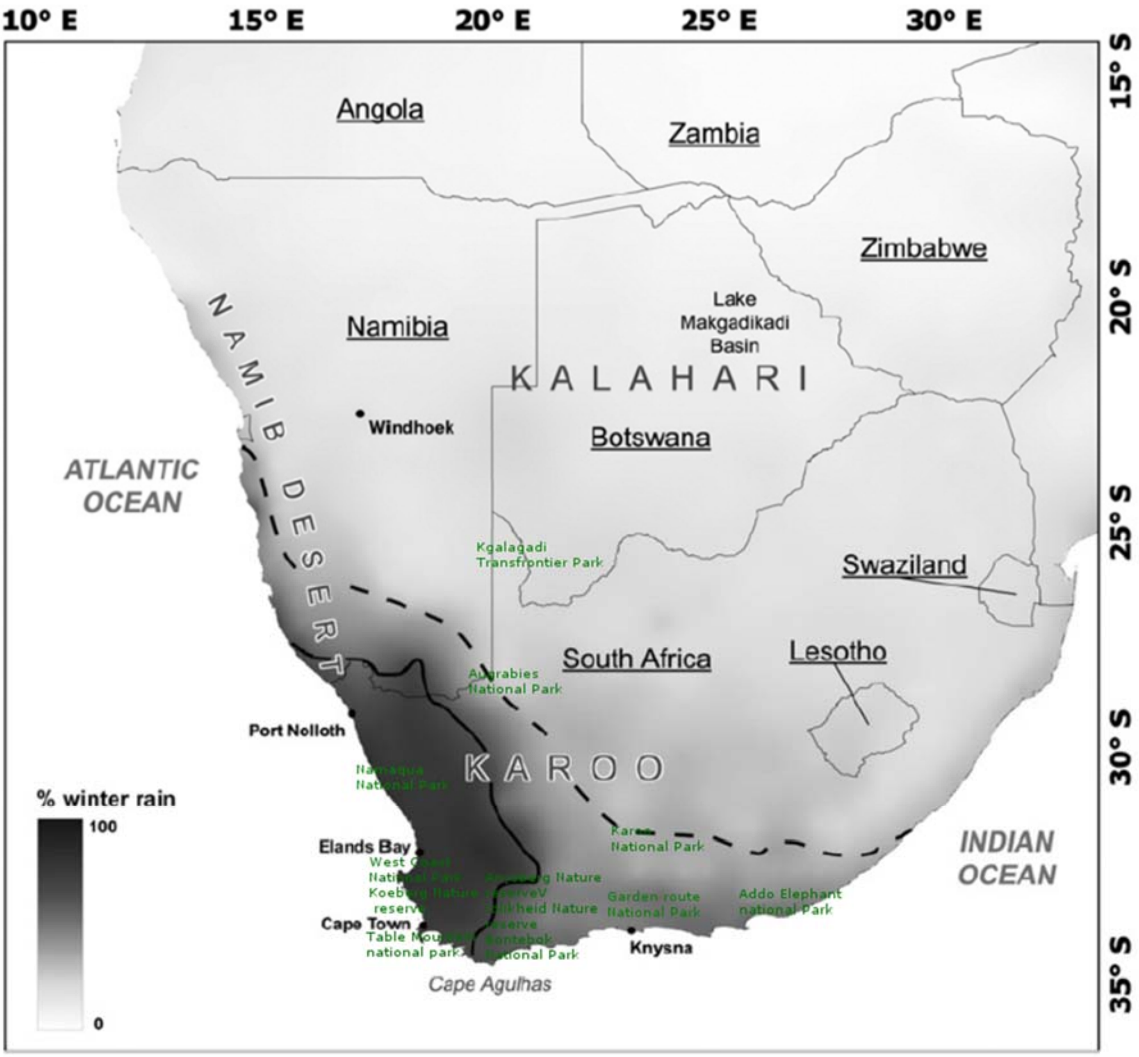

Figure 3. 1 Map showing the percentage rainfall in the winter months (April – September). The solid and dashed lines mark the boundaries of the winter rainfall zone (WRZ) and summer rainfall zone (SRZ) respectively (Chase and Meadows, 2007, Figure 1B, p. 104).

3.2.2 Prevailing weather systems across Southern Africa

The climate in the southwestern region of South Africa is affected by several atmospheric and oceanic systems, especially the high pressure system of the Subtropical South Atlantic Anticyclone (SSAA) and the low pressure system of the Intertropical Convergence Zone (ITCZ) (Figure 3.2). The SSAA has an annual cycle of north-south latitudinal migration of about 6º (Preston-Whyte and Tyson, 1993; Bradshaw and Cowling, 2014). When it is at its northerly position in winter, westerly winds sweep across southwestern Africa, bringing rain and cold temperatures. Thus, winter rainfall develops in and emerges from the west, off the Atlantic Ocean (Van Wyk *et al.*, 2011; Bradshaw and Cowling, 2014). In summer, the SSAA lies further to the south and not only causes the westerly winds move south missing the continent altogether but, being a high pressure system it also prevents moisture from the east penetrating into the winter rainfall areas. This maintains dry conditions in the summer.

Additionally, the SSAA causes upwelling of deep ocean water along the west coast which adds considerably to the aridity of the summer months (Bradshaw and Cowling, 2014).

The ITCZ dominates the summer atmosphere over Southern Africa. This low pressure system enhances evaporation over the Indian Ocean when sea surface temperatures are high. During the summer, the ITCZ is situated in its most southerly position, as shown in Figure 3.2. However, the South African summer rainfall zone is also controlled somewhat by the SSAA high pressure system and the easterly flow of moisture from the Indian Ocean (Preston-Whyte and Tyson, 1993; Bradshaw and Cowling, 2014).

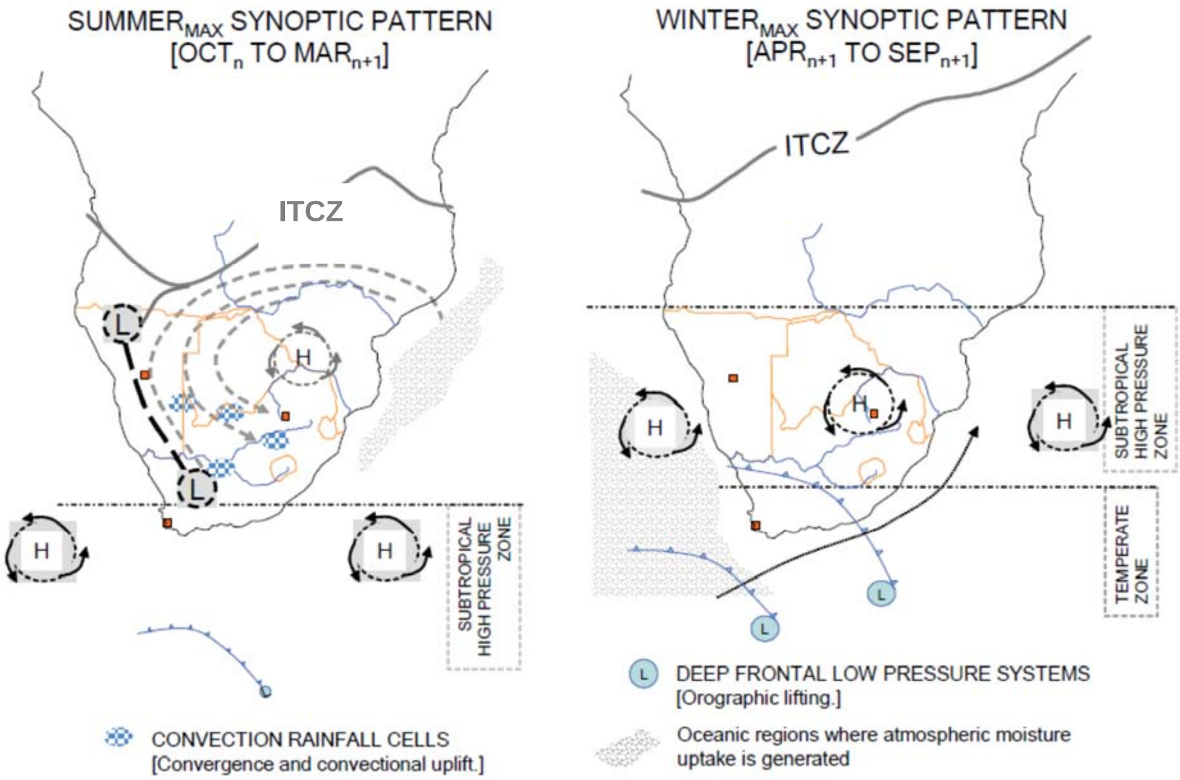

Figure 3. 2: Synoptic patterning over Southern Africa: a comparison between summer and winter months, illustrating the annual south-north migration of the climate zones (Van Wyk *et al.*, 2011, Figure 1, p. 148).

Between these two rainfall zones is an intermediate area which receives rain in both summer and winter (generally referred to as the year-round rainfall zone).

Under modern climatic conditions, westerly winds affect mainly the southwestern portion of Africa, bringing with them winter rain. Current evidence supports the hypothesis that in the past, especially during glacial times when Antarctica sea ice was much expanded, the westerlies would have been displaced equatorward, hence intensifying the winter rainfall regime and expanding the region. One of the key goals of many palaeoclimatic studies in this region is to obtain a better understanding of the types of shifts that occurred under different climatic conditions in the past (Chase and Meadows, 2007, Quick *et al.,* 2016).

3.2.3 Biomes within this region

Biomes are defined by the dominant vegetation type, and the distribution of biomes is controlled largely by climate (Mucina and Rutherford, 2006). Each biome is also divided into bioregions, which are smaller units defined by physical and biotic features (Mucina and Rutherford, 2006). The identification of a specific bioregion is at a higher resolution than biome (there are several bioregions within one biome). By sampling different biomes, one is in effect sampling areas with different climatic conditions. A brief description of each biome is provided with details of any protected areas that fall within them.

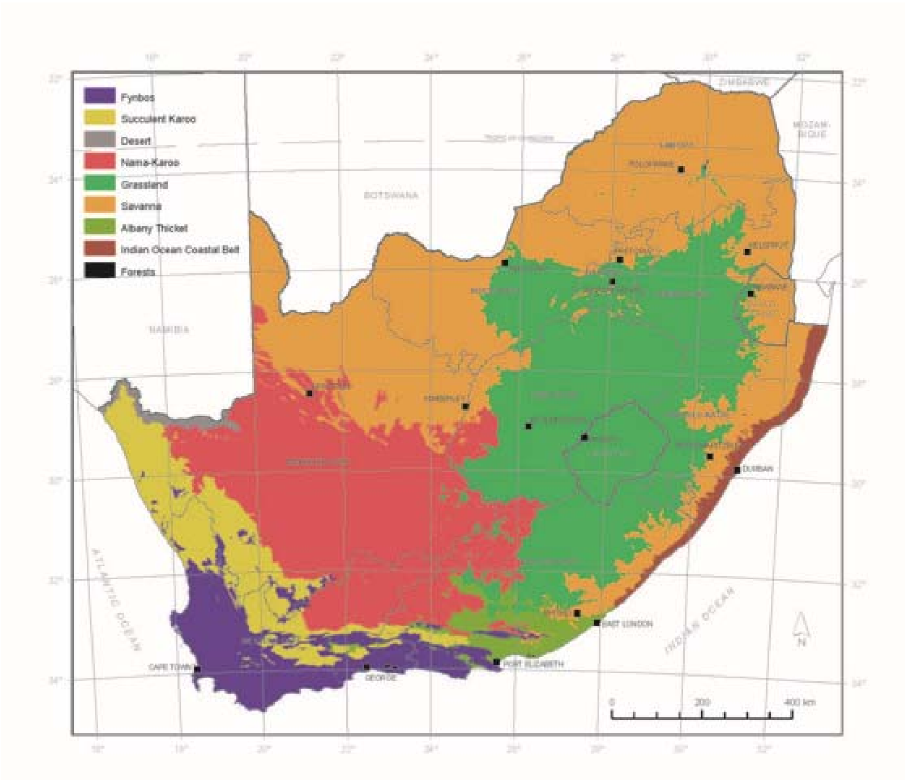

Figure 3. 3 Biomes within South Africa (Mucina and Rutherford, 2006, Figure 3.2, p. 33).

3.2.3.1 Afromontane Forest

The Afromontane Forest biome (will be referred to as “Forest” in this project) occurs in patchy areas with high precipitation and water availability (Mucina and Rutherford, 2006) (Fig. 3.3). The biome is characterised by the dominance of evergreen or semi-deciduous trees that form a closed canopy cover and by shade-tolerant species (Midgley *et al*., 1997; Mucina and Rutherford, 2006). An annual rainfall of above 625 mm is normally required for the development of such forested environments, but this can drop as low as 525 mm in areas that receive winter rainfall (Midgley *et al.,* 1997). In these areas, forest development is controlled by water availability, a function not only of precipitation but also of evapo-transpiration and groundwater availability (Mucina and Rutherford, 2006). However, some have suggested that a summer aridity index is a better predictor for forest occurrence than precipitation (Rutherford and Westfall, 1994).

The largest area of the Forest biome is found on the southern coast of South Africa, where temperatures are moderated by the proximity to the coast. This portion of the biome receives precipitation year round. In terms of vegetation, there is a high frequency of Podocarpaceae, and an abundance of ferns (Figure 3.4) (Midgley *et al.*, 1997). Moreover, the biome is marked by high nutrient levels on the forest floor due to leaf litter and other detritus. The Afromontane Forest has an altitude range of 0-1650m above sea level.

More than half of the southern Forest biome falls within the Garden Route National Park (Mucina and Rutherford, 2006, https://www.sanparks.org). The fauna that occur in this biome thrive in closed canopies and include bushpigs (*Potamochoerus larvatus*), bushbuck (*Tragelaphus scriptus)*, grysbok (*Raphicerus melanotis*), some primates, and many smaller mammals (https://www.sanparks.org; http://www.capenature.co.za/)


a)


b)

Figure 3.4 Landscapes within the Afromontane forest (Garden Route National Park) (Photo a: www.irideafrica.com; Photo b: www.phantomforest.com).

3.2.3.2 Fynbos

The Fynbos biome forms the smallest of the world's floral kingdoms (Mucina and Rutherford, 2006). The climate is primarily controlled by cyclonic cold fronts with north-westerly winds which bring winter rain (Mucina and Rutherford, 2006). The summers are hot and dry caused by high pressure cells and southeasterly winds (Cowling, 1995; Allsopp, 2014). Although highly variable, the mean annual precipitation for the entire region is approximately 480 mm, and it is characterised by acidic, sandy soils. The percentage of summer rainfall and amount of grass increases in northern and eastern regions (Vogel *et al.,* 1978). There are three main taxa within the Fynbos: Proteaceae, Ericaceae and Restionaceae (Figure 3.5). Altitude in this region can be as high as 2000 m.

This biome is highly varied with twelve Fynbos bioregions, some classified as Fynbos and others as Renosterveld (Mucina and Rutherford, 2006). Fynbos bioregions tend to be wetter than Renosterveld bioregions, and some coastal bioregions are very small. This high variability means that some regions receive very low annual precipitation while others receive more. Some regions have very seasonal rainfall while others, such as the Eastern Fynbos-Renosterveld, experience rainfall throughout the year (Mucina and Rutherford, 2006). There are only four bioregions that receive more than 60% of their rain in winter: Southwest Fynbos, Northwest Fynbos, West Coast Renosterveld and West Strandveld (Bradshaw and Cowling, 2014).

The major protected areas that fall within this region include the Table Mountain National Park, West Coast National Park, Bontebok National Park, Agulhas National Park, and several smaller Cape Nature conservation areas including the Cederberg wilderness area and the Grootvadersbosch, Jonkershoek, De Hoop and Vrolikheid Nature Reserves. The Fynbos biome supports relatively few large grazers (Cowling, 1995). Most animals are small browsers that are typically solitary or otherwise live in small groups (https://www.sanparks.org; http://www.capenature.co.za/).

Figure 3. 5 Landscapes within the Fynbos biome (Photos: www.plantzforafrica.com).

3.2.3.3 Succulent Karoo

The Succulent Karoo is a semi-desert biome with a strong oceanic influence, located along the western coast of Southern Africa (Map in Figure 3.3) with some inland areas. This biome is species-rich and has a high diversity of succulent plants (Figure 3.6) (Mucina and Rutherford, 2006). More than 50% of the plants are endemic, and there is a short growing season (Milton *et al.*, 1997). Mean annual precipitation is approximately 170 mm (Mucina and Rutherford, 2006). Most of the biome experiences seasonal rainfall, with the majority of the rain falling in the winter months. Although the amount of rainfall is low, it is consistent and predictable, a trait that is thought to have contributed to the emergence of heightened species richness. Fog is also an important source of water for plants along the coast.

The Succulent Karoo has six bioregions, with the Namaqualand Sandveld bioregion having the lowest mean annual precipitation (100-200 mm). Frost is known to occur in the bioregions nearest the ocean. In particular, the Namaqualand escarpment can have 7-13 episodes of frost in a year (Mucina and Rutherford, 2006). The biome is restricted to areas with less than 250mm of rainfall per annum. In areas where the rainfall is higher, the Succulent Karoo gives way to Fynbos (Cowling, 1995; Cowling *et al.*, 2004).

The Succulent Karoo biome has the following protected areas within it: Namaqua National Park, Hester Malan Nature Reserve, Bereplaas Rolfontein Nature Reserve and Knersvlakte Nature Reserve. The mammal species found in these areas include klipspringer (*Oreotragus oreotragus*), aardvark (*Orycteropus afer*), baboon (*Papio ursinus*), steenbok (*Raphicerus campestris*), duiker (*Cephalophus monticola)*, porcupine (*Hystrix africa-australis*), black-backed jackal (*Canis mesomelas*) and leopard (*Panthera pardus*) (https://www.sanparks.org; http://www.capenature.co.za/).

Figure 3. 6 Landscapes within the Succulent Karoo biome (Photos: www.plantzforafrica.com).

3.2.3.4 Albany Thicket

The Albany Thicket is a semi-arid biome characterised by year-round rainfall (See map in Fig. 3.3 for location). Rainfall is irregular, though it usually peaks in the spring and autumn months. High temperatures, at times exceeding 40°C, occur in summer. Due to the inconsistent rains as well as increased temperatures, some resident plants have evolved succulence in order to adapt to these climatic extremes (Mucina and Rutherford, 2006).

The Albany Thicket is marked by a high diversity of plant species which include leaf and stem succulents, woody and dwarf shrubs, geophytes, annuals and grasses (Figure.3.7) (Cowling, 1995; Cowling *et al*., 2003; Cowling *et al.*, 2004). Spekboom (*Portulacaria afra*) is an abundant succulent species that is heavily browsed by animals. In general, the flora is short (approximately 2-3 m in height), dense, impenetrable and thorny (Mucina and Rutherford, 2006). More broadly, this biome contains elements of the Savanna, Nama-Karoo and Afromontane Forest biomes. Height above sea level ranges from 250-970 m.

The most significant protected area that falls within this biome is the Addo Elephant National Park. Of particular interest is that the main section of the park has no natural water and most waterholes are fed by boreholes (https://www.sanparks.org). There are a number of small pans in the area, but these are often dry except in years marked by exceptionally high rainfall. The fauna in the park include large herds of elephant and buffalo. There are also carnivores, such as lion and spotted hyena, which were re-introduced to the park in 2003. There are large numbers of other ungulates including red hartebeest (*Alcelaphus buselaphus*), eland (*Tragelaphus oryx*), kudu (*Tragelaphus strepsiceros*), bushbuck (*Tragelaphus scriptus*), Burchell's zebra (previously E*quus burchelli* and now referred to as *Equus quagga*) and warthog (*Phacochoerus africanus*) (https://www.sanparks.org; http://www.capenature.co.za/).

Figure 3. 7 Landscapes within the Albany Thicket biome (Photos: J and S Luyt).

3.2.3.5 Nama Karoo

The Nama Karoo biome is a large, central, land-locked biome (Figure 3.3). Mean annual precipitation is approximately 200 mm (range 40-400 mm), with most rain falling in the summer, particularly the late summer months (Mucina and Rutherford, 2006). Rainfall is highly variable in both form and extent and is unpredictable in its occurrence. This biome is very arid and is characterised by the dominance of dwarf, open scrubland (Figure 3.8) (Palmer and Hoffman, 1997). Most of the rivers in the Nama Karoo are non-perennial (Mucina and Rutherford, 2006).

There are three bioregions in the Nama Karoo, none of which are influenced by the ocean (Mucina and Rutherford, 2006). In general, the biome has low species diversity, and the various vegetation types are, for the most part, evenly spread across the three bioregions. Most of the biome is between 550 m and 1500 m above sea level (Palmer and Hoffman, 1997).

The protected areas that fall within the Nama Karoo include Augrabies National Park, Karoo National Park, Anysberg Nature Reserve, and also some smaller Cape Nature protected areas.

This unpredictable and arid biome favours animals that can cope under hardy conditions, including ostriches (*Struthio camelus*), gemsbok (*Oryx gazella*) and springbok (*Antidorcas marsupialis*). The biome also has small numbers of red hartebeest (*Alcelaphus buselaphus*), duiker (*Cephalophus monticola*), steenbok (*Raphicerus campestris*) and grysbok (*Raphicerus melanotis)* (https://www.sanparks.org; http://www.capenature.co.za/)..

Figure 3. 8 Landscapes within the Nama Karoo biome (Photos: www.plantzafrica.com).

3.2.3.6 Savanna

The savanna biome is the largest biome of Africa, though only the southern extent of this biome occurs in South Africa (Figure 3.3). The climate of the savanna is characterised by hot, wet summers (ranging from four to eight months in length) and warm, dry winters (Scholes, 1997). The savanna is characterised by tropical vegetation composed of both woody plants and grasses (Figure 3.9). Tree canopy cover in such environments can range from 5-90% (Scholes, 1997). The savanna biome transitions to the Nama Karoo biome in the south and west as water availability decreases and trees give way to shrubs (Scholes, 1997). Regardless of the shift in conditions between the two biomes, they share many species of vegetation.

Although the savannah biome has six bioregions, only one falls within the study area: the Kalahari Duneveld bioregion. The mean annual precipitation in this bioregion is 184mm (range 120-260 mm) (Mucina and Rutherford, 2006). The Kalahari Duneveld receives the lowest mean annual precipitation and is at the highest altitude of any savanna bioregion (1500-1800m above sea level) (Mucina and Rutherford, 2006). This region has the lowest number of vegetation types and is distinctly unlike the rest of the savanna biome, which is more woodland-based (Mucina and Rutherford, 2006). In fact, some researchers do not place the Kalahari Duneveld in the savanna biome at all (Rutherford, 1997), preferring instead to label it the Nama Karoo since the vegetation is so similar.

The Kgalagadi Transfrontier Park falls within the Kalahari Duneveld. The fauna found in this biome include grazing and browsing herbivores (such as eland (*Tragelaphus oryx*), gemsbok (*Oryx gazella*), and blue wildebeest (*Connochaetes taurinus*)) and carnivores (such as lions (*Panthera leo*), leopards (*Panthera pardus*) and hyenas (*Crocuta crocuta* and *Hyaena brunnea*)).

Figure 3. 9 Landscapes within the Kalahari Duneveld (photos: J and S Luyt).

3.3 Environmental data

For each bioregion, environmental data were collected from the literature. The variables chosen were: mean annual precipitation (MAP[7]), mean annual temperature (MAT[8]), mean

[7] Defined as the arithmetic mean of the precipitation at bioregion level over the 34 year period from 1 January 1960 to 31 December 1993 (Mucina and Rutherford, 2006).
[8] Defined as the temperature of the whole year arithmetically averaged over the 34 year period from 1 January 1960 to 31 December 1993, at bioregion level (Mucina and Rutherford, 2006).

annual soil moisture stress (MASMS[9]), mean annual potential evapotranspiration (MAPE[10]), relative humidity (RH), summer aridity index (SAI[11]), winter concentration of rainfall (WCR[12]), moisture index (MI[13]) and water deficit (WD[14]).

MAP, MAT, MAPE and MASMS data were obtained from Mucina and Rutherford (2006). They used data for a 34 year period from 1 January 1960 to 31 December 1993 which was gathered from Schulze (1997).

Seasonality of rainfall indices were calculated based on monthly rainfall. These indices were first defined by Rutherford and Westfall in 1994. Data on monthly precipitation (used to calculate SAI and WCR) were obtained from the South African Weather Service, using the most suitable weather station nearest to each region. RH was also obtained from the South African Weather service. These data were for the year 2013. This is raised as a substantial limitation of the current study. In future, these values should be averaged over at least 10 years. Looking at one particular year means annual fluctuations are not accounted for. Also, there were few weather stations available in the study region and as such the distance of the nearest station varied. This spatial resolution is a difficult issue since the sources of meteorological variables are different. Unfortunately using environmental data at this scale does gloss over smaller scale variability but since the application here is palaeo-environmental reconstruction this broader approach is reasonable.

Some indices were included that take into account two climatic variables: WD and MI. The WD was included for comparability with Levin *et al.* (2006), who use this measure. The MI provided an indirect bioclimatic measure of annual plant water availability (Gallego-Sala *et al.,* 2010; Harrison *et al.,* 2010) so that the higher the MI value, the more moisture was present in the environment.

The environmental variables for each of the bioregions and collection locations within each biome are provided in Appendix 2. Spearman's rho correlations (nonparametric version of the Pearson product-moment correlation) were carried out on all variables in order to measure the

[9] Defined as the % days when evaporative demand was more than double the soil moisture supply (Mucina and Rutherford, 2006).
[10] Defined as the the average annual amount of evaporation that would occur if sufficient water were available.
[11] Defined as the sum of the mean precipitation of the four hottest months of the year (Dec – March) (Rutherford and Westfall, 1994).
[12] Defined as the percentage of MAP received during the winter half year (April – September) (Rutherford and Westfall, 1994).
[13] Defined as the mean annual precipitation divided by the mean annual potential evapotranspiration (Harrison *et al*., 2010).
[14] Defined as the PET (potential evapotranspiration) – MAP (mean annual precipitation) (Levin *et al.,* 2016).

strength of association between each pair of ranked variables. The results are presented in Appendix 3. Many of these environmental measures exhibited significant correlations, which had implications for the choice of statistical methods used in analysing the isotopic data. This issue is discussed in more detail in the Data analysis section 4.5.

3.4 Summary

This chapter provided an overview of the study region and the attributes of each of the biomes and bioregions. The range and types of environmental data used in the analysis of the isotopic measurements was also described. Each biome is a distinct bioclimatic space characterised by several and often distinct climatic variables.

Chapter 4: Materials and Methods

4.1 Introduction

In this study, isotopic analyses were performed on the bone and tooth enamel of herbivores, primates and carnivores from natural, contemporary environments. This chapter will outline how faunal specimens were obtained and how samples were taken for isotopic analysis. Laboratory techniques used to prepare bone collagen and enamel will be described, followed by the procedures used in the mass spectrometry laboratory to measure the isotope ratios. Finally, the statistical methods used to assess the results will be outlined.

4.2 Sampling approach

Faunal specimens were obtained from three sources. The first source was parks and protected areas managed by SanParks and Cape Nature. Specimens were collected in terms of the requisite permits (see Appendices 1 and 2). Collection was limited to animals that had died between January 2013 and July 2015. The bulk of the samples were obtained from this source. Care was taken to avoid collecting animals known to have been translocated since their isotopic composition would not reflect the local environment. The second source was material that had previously been collected and curated within the Department of Archaeology at UCT. The third source was donations from private individuals.

For curated and donated specimens, care was taken to include only animals that lived in natural environments (i.e., those that did not have access to artificial feed, cultivated crops, etc.). Adult animals were sampled whenever possible, but in some cases juveniles were also included; these represent a small fraction of the total, and are identified as juveniles in the results.

A list of ungulate species sampled is provided in Table 4.1 while the list of carnivore and primate species sampled are in Table 4.2. Figure 4.1 indicates the locations of all specimens.

Table 4. 1 List of ungulate species sampled in the study region by biome. Biome: F=Fynbos; AT = Albany Thicket; FO, Forest; NK = Nama Karoo; S=Savanna; SK = Succulent Karoo. Water behaviour: WI= Water insensitive; WD= Water dependent. Evaporation sensitivity: EI = Evaporation insensitive; ES= Evaporation sensitive. Type of fermenters = R=Ruminant; H = Hindgut. Size: EL= Extra large; L= Large; M=Medium; S= Small)

Order	Family	Species	Common name	Biome	Feeder Type	Water behaviour	Evaporation sensitivity	Size	Type of fermenters	N sampled
Proboscidea	Elephantidae	*Loxodonta africana*	Elephant	Fo	B	WD	EI	EL	H	1
Perissodactyla	Rhinocerotidae	*Diceros bicornis*	Black Rhino	NK	B	WD	EI	EL	H	1
Perissodactyla	Equidae	*Equus burchelli*	Burchell's Zebra	SK	G	WD	EI	L	H	1
Perissodactyla	Equidae	*Equus zebra*	Mountain zebra	F	G	WD	EI	L	H	1
				SK	G	WD	EI	L	H	2
Suiformes	Suidae	*Phacochoerus africanus*	Warthog	AT	G	WI	EI	M	H	7
Suiformes	Suidae	*Potamochoerus larvatus*	Bushpig	Fo	O	WD	EI	M	H	13
				F	O	WD	EI	M	H	1
Whippomorpha	Hippopotamidae	*Hippopotamus amphibius*	Hippopotamus	Fo	G	WD	EI	EL	R	3
Ruminatia	Giraffidae	*Giraffa camelopardalis*	Giraffe	NK	B	WD	ES	EL	R	2
				S	B	WD	ES	EL	R	1
Ruminatia	Bovidae	Alcelaphine	Bontebok/Hartebeest	F	G	WI	EI	L	R	7
Ruminatia	Bovidae	*Alcelaphus buselaphus*	Red hartebeest	AT	G	WI	EI	L	R	19
				F	G	WI	EI	L	R	12
				NK	G	WI	EI	L	R	1
				S	G	WI	EI	L	R	4
				SK	G	WI	EI	L	R	5
Ruminatia	Bovidae	*Antidorcas marsupialis*	Springbok*	F	M	WI	ES	M	R	27
				NK	M	WI	ES	M	R	23
				S	M	WI	ES	M	R	4
				SK	M	WI	ES	M	R	14
Ruminatia	Bovidae	*Cephalophus monticola*	Blue duiker*	Fo	B	WI	ES	S	R	3
Ruminatia	Bovidae	*Connochaetes taurinus*	Blue wildebeest	S	G	WD	EI	L	R	11
Ruminatia	Bovidae	*Damaliscus pygargus pygarus*	Bontebok*	F	G	WD	EI	M	R	5
				S	G	WD	EI	M	R	1
Ruminatia	Bovidae	*Oreotragus oreotragus*	Klipspringer	F	B	WI	ES	S	R	2
				NK	B	WI	ES	S	R	1
				SK	B	WI	ES	S	R	2
Ruminatia	Bovidae	*Oryx gazella*	Gemsbok*	S	G	WI	EI	L	R	17
				SK	G	WI	EI	L	R	24
Ruminatia	Bovidae	*Pelea capreolus*	Grey rhebuck	F	B	WI	ES	S	R	1
				SK	B	WI	ES	S	R	1
Ruminatia	Bovidae	*Raphicerus campestris*	Steenbok*	F	B	WI	ES	S	R	6
				S	B	WI	ES	S	R	1
				SK	B	WI	ES	S	R	2
Ruminatia	Bovidae	*Raphicerus melanotis*	Grysbok*	Fo	B	WI	ES	S	R	3
				F	B	WI	ES	S	R	6
Ruminatia	Bovidae	*Raphicerus sp*	Steenbok/Grysbok	Fo	B	WI	ES	S	R	1
				SK	B	WI	ES	S	R	7
Ruminatia	Bovidae	*Redunca arundinum*	Southern reedbuck	AT	G	WD	EI	M	R	1
				NK	G	WD	EI	M	R	1
Ruminatia	Bovidae	*Sylvicapra grimmia*	Common duiker*	F	B	WI	ES	S	R	12
				SK	B	WI	ES	S	R	21
Ruminatia	Bovidae	*Syncerus Caffer*	Buffalo*	AT	G	WD	EI	L	R	26

Order	Family	Species	Common name	Biome	Feeder Type	Water behaviour	Evaporation sensitivity	Size	Type of fermenters	N sampled
				Fo	G	WD	EI	L	R	1
Ruminatia	Bovidae	*Tragelaphus oryx*	Eland	AT	B	WI	ES	L	R	9
				Fo	B	WI	ES	L	R	3
				NK	B	WI	ES	L	R	3
				S	B	WI	ES	L	R	19
				SK	B	WI	ES	L	R	1
Ruminatia	Bovidae	*Tragelaphus scriptus*	Bushbuck	AT	B	WD	ES	M	R	5
				Fo	B	WD	ES	M	R	6
Ruminatia	Bovidae	*Tragelaphus strepsiceros*	Kudu*	AT	B	WD	ES	L	R	9
				NK	B	WD	ES	L	R	1
				SK	B	WD	ES	L	R	1

* Tooth-row comparisons were performed on these species.

Table 4. 2 List of primate and carnivore species sampled in the study region by biome. * Tooth-row comparisons were performed on these species.

Order	Family	Species	Common name	Biome	Type	Feeder Type	N sampled
Primates	Cercopithecidae	*Chlorocebus pygerythrus*	Vervet monkey	Fo	Primate	Omnivore	2
Primates	Cercopithecidae	*Papio ursinus*	Baboon	AT	Primate	Omnivore	8
				FO	Primate	Omnivore	9
				F	Primate	Omnivore	79
				SK	Primate	Omnivore	49
Carnivora	Canidae	*Canis mesomelas*	black-backed jackal*	F	Primate	Omnivore	2
				S	Carnivore	Carnivore	1
Carnivora	Canidae	*Otocyon megalotis*	Bateared fox	Fo	Carnivore	Insectivore	1
				NK	Carnivore	Insectivore	1
Carnivora	Canidae	*Vulpes chama*	Cape fox	F	Carnivore	Carnivore	1
Carnivora	Hyaenidae	*Crocuta crocuta*	Spotted hyena	AT	Carnivore	Carnivore	1
				S	Carnivore	Carnivore	1
Carnivora	Hyaenidae	*Hyaena brunnea*	brown hyena	S	Carnivore	Carnivore	3
Carnivora	Hyaenidae	*Proteles cristata*	Aardwolf	F	Carnivore	Insectivore	1
Carnivora	Felidae	*Felis caracal*	Caracal*	Fo	Carnivore	Carnivore	2
				F	Carnivore	Carnivore	3
				S	Carnivore	Carnivore	2
Carnivora	Felidae	*Panthera leo*	Lion	AT	Carnivore	Carnivore	1
Carnivora	Felidae	*Panthera pardus*	leopard	Fo	Carnivore	Carnivore	1
				F	Carnivore	Carnivore	7
				S	Carnivore	Carnivore	1
				SK	Carnivore	Carnivore	1
Carnivora	Viverridae	*Genetta genetta*	Common genet	Fo	Carnivore	Carnivore	1
Carnivora	Mustelidae	*Mellivora capensis*	Honey badger	Fo	Carnivore	Carnivore	2

* Tooth-row comparisons were performed on these species.

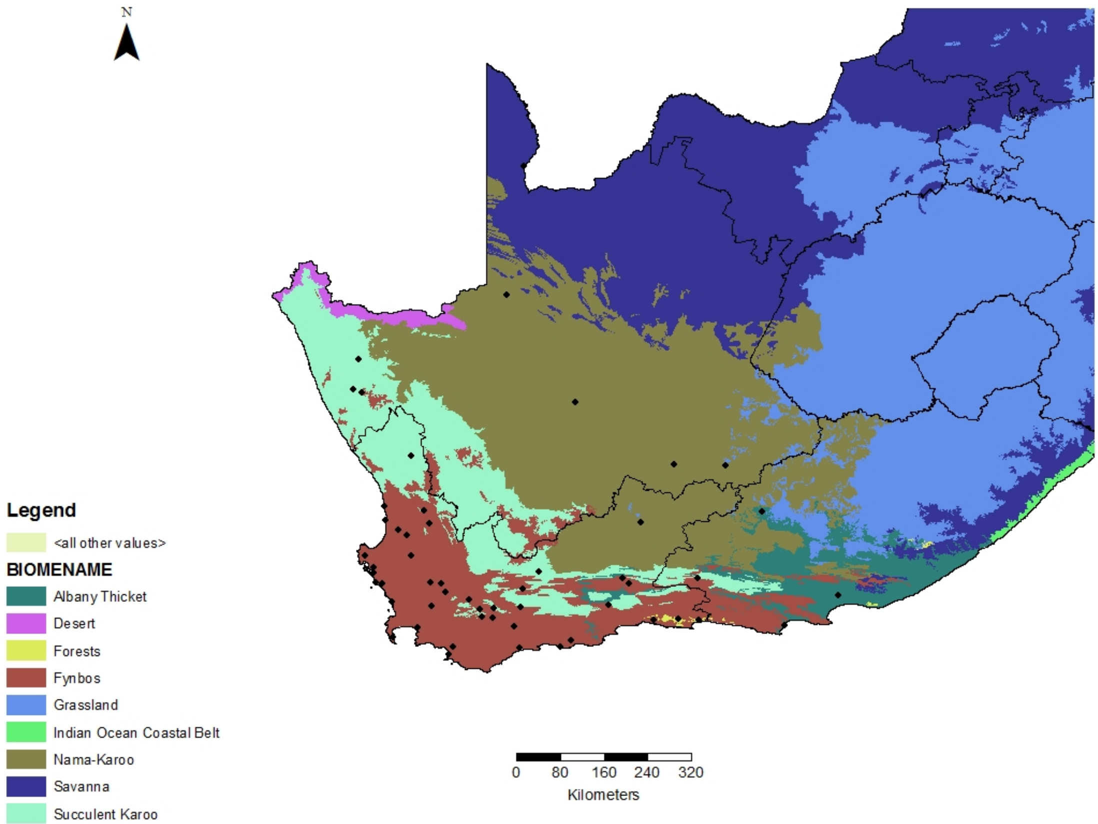

Figure 4. 1 Map showing sample collection sites overlaid on biomes.

A major limitation of this study was the length of time available for collection. I had only had two years to collect samples (2013-2014), where ideally this should have been done over at least ten years. Thus I was limited by the number of animals that died (and were found in the field) doing the collection period. The time available for collection impacted sample size. Once the data was separated into biomes and then species, the sample sizes were lower than hoped for. A possible extension of this project could be to compare a single species across environmental gradient, to eliminate all other behavioural factors. In this case one could also choose only to analyse one particular tooth to further limit inter-tooth variation. With larger sample sizes, one could work at higher spatial resolution and not analyse the meteorological variables at biome level. Although sample sizes will be increased having specimens that died over ten years might include alternating climate patterns within each biome, which may complicate the objective of looking at climate differences across biomes (Codron, D., 2016, pers. comm., 31 October).

Due to the low numbers across biomes, animals were grouped together (grazers, browsers, etc.). Thus, a further limitation is in the dietary classification of these groups. These groups contain a fair amount of variation and herbivores are far more complex than the four dietary groups that are normally assigned.

4.3 Sampling procedures

Samples of bone and tooth enamel were taken from each animal when available. A hand-held rotary drill fitted with a 0.5 mm diameter diamond-tipped dental drill bit was used to collect 5-10 mg of enamel powder. The tooth was drilled from the occlusal surface to the cervix to collect enamel representative of the entire period of crown formation in order to average out seasonal variations. For the purposes of this project, I chose not to investigate seasonal variability, but rather to obtain an integrated isotopic value for the entire period of tooth formation. In order to limit intra-individual variation, enamel from the first molar (M1) was sampled. If this was not possible, the second or third molars were sampled (Table 4.1).

For approximately 50 animals, samples of enamel were taken from multiple teeth in order to investigate changes in $\delta^{13}C$ and $\delta^{18}O$ as the animal matured. These were animals for which hemi-mandibles or maxillae were available. Samples of enamel were taken from each tooth along the tooth row to detect any changes in the diet as the animal matured or any environmental changes that occurred during the animal's life, such as seasonal changes in forage or water availability. Developing this baseline will be helpful to researchers constrained by limited choice of teeth in archaeological assemblages. Species for which a series of samples were taken along the tooth row are marked by an asterix in Table 4.1 and Table 4.2.

In order to measure carbon and nitrogen isotopes in bone collagen, 10-150 mg of bone were sampled from the cranium of an individual. Crania were sampled in order to be certain that the bone and tooth samples derived from the same animal since material obtained from nature reserves sometimes consisted of multiple co-mingled individuals. In cases where crania were not available, other skeletal elements were sampled. Bone samples were cut using a Dremel drill fitted with an emery cut-off wheel.

4.4 Laboratory techniques

4.4.1 Preparation of enamel

Enamel was prepared using the method described in the following papers (with some modifications): Lee-Thorp *et al.* (1997) and Sponheimer and Lee-Thorp (1999b). Approximately 10 mg of enamel powder was treated with 1 ml of ~1,75% v/v sodium hypochlorite for 45 minutes to remove organic contaminants. The samples were then centrifuged and rinsed three times with distilled water. Next, they were treated with 0.1M acetic acid for 15 minutes to remove any soluble mineral components. These included adsorbed carbonates, which are more soluble than structural carbonates and thus could be removed effectively in this way (Webb *et al.*, 2014). Calcite contamination was also removed. The samples were again centrifuged and rinsed three times with distilled water before being freeze-dried.

4.4.2 Determination of $\delta^{13}C$ and $\delta^{18}O$: Instrumentation and standards

Approximately 2 mg of dry, pre-treated enamel powder was weighed into a 12 ml borosilicate glass tube capped with a screw top lid with septum. The tubes were placed in a Thermo Finnigan Model II gas bench in a temperature controlled sampler tray set to 72°C. Using the CTC Analytics A200S auto sampler, the tubes were flushed with helium. Five to seven drops (according to sample size) of 100% H_3PO_4 were then manually added to each sample tube through the septum using a syringe. The samples were left for a minimum of two and a half hours for the carbonate in the apatite to react with the 100% H_3PO_4 to release CO_2. The gas evolved in each tube was sampled by the auto sampler. Gas was then passed through a Nafion water removal unit followed by a "Poraplot Q" gas chromatographic column and then through a second Nafion water trap. Finally, the purified CO_2 was measured by a Delta Plus XP isotope ratio mass spectrometer (IRMS) (Thermo electron, Bremen, Germany) controlled by Isodat software.

Precision was monitored by repeated analysis of internationally recognised standard materials. Two standard calcites (NBS18 and NBS19) and an internal standard (Cavendish Marble) were included in each run. The $^{13}C/^{12}C$ and $^{16}O/^{18}O$ ratios were reported in the standard δ notation relative to the PeeDee Belemnite (PDB, a marine sedimentary carbonate) standard in parts per mil (‰). The reproducibility of repeated measurements of the standard materials was ≤ 0.2‰ for both carbon and oxygen for all runs except one. Appendix 4a reports the values of the repeated standard measurements, thus demonstrating the instrument precision.

4.4.3 Extraction of bone collagen

Each bone sample was mechanically surface cleaned and weighed to enable determination of the collagen yield. The samples were then soaked overnight at room temperature in a de-fatting solution of chloroform, methanol and water (2.0:1.0:0.8 v:v). Most lipids were removed by this solution and floated to the top of the liquid. The de-fatting solution was poured off and the de-fatting process was repeated if large quantities of lipids were observed. All samples were then rinsed with distilled water.

Samples were then soaked in dilute HCl at room temperature in order to remove the apatite from the bone. The molarity of the dilute HCl ranged from 0.1M to 0.5M, depending on the size and density of the bone fragment. The concentration of the acid should not have influenced the isotope values of the collagen (Pestle, 2010). The acid was changed every day for between two days to fourteen days, depending on the size of the sample and the density of the bone. This resulted in a translucent, flexible pseudomorph of (mostly) collagen of the same shape and size as the original bone fragment.

Each pseudomorph was soaked in in 0.1M NaOH overnight to remove base-soluble contaminants such as humic acids and any remaining lipids (Ambrose, 1990). Next, the samples were soaked in distilled water, which was changed daily until its pH remained neutral. The sample was then freeze-dried. After freeze-drying, they were allowed to equilibrate with the atmosphere (overnight) before being weighed to obtain the mass of collagen extracted. The mass of collagen was expressed as a percentage of the initial weight of the bone sample to give the collagen yield.

There has been some discussion in the recent literature concerning the advantages and disadvantages of different methods of collagen preparation. The “chunk” method described here has been extended, in many laboratories, to include dissolving the collagen pseudomorph in very dilute acid (“gelatinisation”), which is sometimes followed by ultra-filtration in order to isolate only higher molecular weight protein fragments (Longin, 1971; Brown *et al.,* 1988; Brock *et al*., 2010). These modifications were originally introduced so as to isolate pure collagen used for radiocarbon dating from highly contaminated and/or degraded samples. These protocols have since become widely used in stable isotope laboratories (van Klinken and Hedges, 1995; O'Connell *et al*., 2001). Sealy *et al.* (2014) recently compared the two methods by performing both the ‘chunk’ and gelatinisation and ultrafiltration on over 50 samples of well-preserved archaeological bone. The authors found that there was no statistical differences in the collagen quality indicators (discussed in the next section), nor in $\delta^{13}C$ and $\delta^{15}N$ measurements on collagen obtained using the two methods (Sealy *et al.*, 2014). They concluded that for well-preserved bones, the “chunk” method continues to be an acceptable method for extracting collagen. This method was therefore used to extract collagen from the modern bones analysed in this study. The quality of the extracted collagen was evaluated by assessing collagen yield, carbon to nitrogen ratios and carbon and nitrogen concentrations (reported in Appendix 5).

4.4.4 Determination of $\delta^{13}C$ and $\delta^{15}N$: Instrumentation and standards

For each sample, approximately 0.5 mg of extracted collagen was weighed into a tin cup. Tin was used because it melts at 235^0C with very low enthalpy (heat content) and mixes effectively with organic substances, thus expediting the oxidation of the collagen.

The samples were combusted in a Flash EA 1112 series elemental analyser (Thermo Finnigan, Milan, Italy). The gases were passed through to a Delta Plus XP IRMS (Thermo electron, Bremen, Germany), via a Conflo III gas control unit (Thermo Finnigan, Bremen, Germany). Samples were analyzed in duplicate and, in most cases, in different runs. If the values of the duplicates differed by more than 1‰ then the samples were re-analysed. If this was not possible, the results were discarded; seven out of 479 samples were discarded accordingly (1.4%).

In each run, in-house standards (Valine, Merck Gel and Seal bone) were analysed in order to assess instrument precision. Each standard had been calibrated against international standard materials NBS 21, IAEA N1 and N2 and standards exchanged with other laboratories. The reproducibility of repeated measurements of these standard materials was ≤ 0.1‰ for both carbon and nitrogen for all runs except four, where reproducibility was ≤ 0.2‰ (Appendix 4b).

4.4.5 Quality indicators [15]

The bone samples all yielded pseudomorphs, an indicator of structural integrity. The weights, N%, C%, collagen yields and C:N ratios were analysed for all samples to determine whether they had undergone significant diagenesis and whether they were of an acceptable quality for further analysis (Appendix 5). Yields for bone collagen ranged between 5% and 34%, which is within an accepted range for reliable carbon and nitrogen isotope analysis (Ambrose, 1990).

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[15] Modern bones from a temperate environment such as the winter rainfall zone of Southern Africa are unlikely to have undergone significant diagenesis, although it has been documented in cases where material has been exposed to the surface in very harsh environments (Tuross *et al.*, 1988). Collagen quality indicators are reported here (and in detail in Appendix 5) because it is valuable to have a dataset that documents the range of variation in these indicators in well-preserved modern bones. In addition, since the presence of lipids leads to elevated C% and C/N ratios, monitoring C% and C/N ratios also confirms that lipids have been successfully removed from the samples. Bone collagen preservation varies across the globe with preservation rates in tropical regions differing from those in more temperate environments (Van Klinken, 1999). Bone degradation begins with a disintegration of the bonds between the amino acids. The peptides are then lost from the helical structure and finally are leached from the bone (Van Klinken, 1999). Degraded bone can be identified by infra-red spectroscopy but the most effective method is monitoring the collagen yield (collagen as weight percentage of the bone before demineralisation). The collagen content of modern fresh bone is 20-30%. Ambrose (1990) showed that for archaeological material, the stable carbon and nitrogen isotope ratios could be measured reliably in specimens with collagen yields down to 3.5%. A second indicator of quality is the carbon-to-nitrogen (C:N) ratio of the extracted collagen. Since glycine (which makes up every third amino acid within a collagen chain) has only two carbon atoms and one nitrogen atom (most other amino acids have four or more carbon atoms), the atom-to-atom ratio of C:N in collagen is about 3:1. In other proteins, the C:N ratio is closer to 5:1. Therefore, a low C:N ratio is considered one of the diagnostic features of collagen with any deviating values considered to indicate alteration (Schwarcz and Schoeninger, 1991). Van Klinken (1999) uses a range of 3.1-3.5 for acceptable samples while De Niro (1985) suggests a wider range of 2.9-3.6.

The C:N ratios of collagen extracts ranged between 3.2 and 3.6 (within the accepted range for well-preserved bone; De Niro, 1985; van Klinken 1999) except for three specimens which yielded C:N ratios outside of this range for both duplicates and were therefore removed from the analysis.

4.5 Data analysis

For all isotopes ($\delta^{13}C_{collagen}$, $\delta^{18}O$, $\delta^{13}C_{enamel}$ and $\delta^{15}N$) the data were divided to look at differences by biome and dietary preference. Categories of dietary preference were: ungulates, carnivores or primates. Ungulates were further divided into browser, grazers, mixed feeders or omnivores. Ungulates were further defined as: evaporation insensitive or evaporation sensitive; water dependent or water independent; ruminant and non-ruminant; and extra large[16], large[17], medium[18] and small[19] (refer to Table 4.1 for ungulates and Table 4.2 for primates and carnivores). As discussed in Chapter 2, animals that were consuming foods that would be affected by meterological factors, such as levels of evapoaration, were found to vary along with the $\delta^{18}O$ leaf values of the plants they were consuming (Ayliffe and Chivas, 1990; Levin *et al.,* 2006). Thus evaporation sensitivity was predicted to influence $\delta^{18}O$, with low values indicating a cooler environment and high values indicating a more arid environment (Levin *et al.* 2006). In this manner, all ungulates were labelled as either evaporation sensitive or evaporation insensitive. Classifying animals in this way can be problematic because whether an animal is water dependent or water independent or evaporation sensitive or insensitive is far from resolved. For the purposes of this thesis is it reasonable to use the same categorisations used by previous workers (especially Levin *et al.,* 2006) so that comparisons can be made.

For $\delta^{15}N$ only, the size of animal and whether it was ruminant or non-ruminant were thought to be of importance. Thus ungulates were also subdivided into these groups for analysis (Table 4.1).

Data distribution was tested using both Shapiro-Wilk and Kolmogorov-Smirnov tests. Data analyses were conducted using SPSS (Version 23). Results of these tests are provided in Appendix 6. The data were non-normal and, when broken down into animal feeding types, four of the five groups in the dataset were non-normally distributed. Since this was the case, non-parametric tests were used in evaluating the data. The one category that routinely

[16] Average weight >900kg
[17] Average weight 120 – 860 kg
[18] Average weight 30 – 110 kg
[19] Average weight <30kg

demonstrated normally distributed values was the carnivore subset, which was also the smallest group. It may be that small sample size influenced these results.

Kruskal-Wallis H one-way tests were run for each of the carbon, nitrogen and oxygen datasets. Pairwise comparisons with adjusted p-values[20] were used to demonstrate which sub groups within the datasets were different. If only two groups existed (for example ES vs. EI) then Mann-Whitney tests were used. If there were more than two groups, Kruskal-Wallis one-way tests were used to determine if groups were different, while the Wilcoxon test was used to indicate which groups these were. All analyses were performed on SPSS. A *p*-value of <0.05 indicated a significant difference.

Regression models were run to investigate the relationships between isotopes, and to estimate the degree of change in isotope values in response to variations in meteorological factors. Univariate regression models (ANCOVA, displayed as 'General Linear model' in SPSS) were run for each isotopic value ($\delta^{13}C_{enamel}$, $\delta^{18}O_{enamel}$, $\delta^{13}C_{collagen}$, $\delta^{15}N_{collagen}$) against each meteorological factor (MAP, MAT, MASMS, MAPE, RH, SAI, WCR, WD and MI) in turn. Where more than one tooth per animal was analysed, a single average value was used since regression analyses require that all data points are of the same type (i.e., all averages or all individual results). For ungulates, two fixed variables were included: feeder type and animal size. Adjusted r^2 values were used to account for the number of predictors in the model. Correlation coefficients were considered significant at the $p<0.05$ level.

Since many of the meteorological factors are highly correlated and regression assumes no relationship between variables, this needed to be accounted for in models that used more than one variable. The approach used here to identify the best model in the presence of multicollinearity was to look at the correlations previously tabulated (Appendix 3). Pairs of meteorological factors that had multicollinearity problems were discarded. The model with the lowest Akaike information criterion[21] (AIC - a measure of the relative quality of statistical models for a dataset) was selected.

The aridity index (cf Levin *et al.,* 2006) was calculated by comparing the average values for the evaporation sensitive/insensitive (ES and EI) groups and also the water dependent/independent groups. The aridity index was the difference between the two groups (ES – EI and WI – WD).

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[20] Adjusted p values adjust the p value to account for the number of tests done. It does this by adjusting the p-value down to make sure that the chance of making a Type I error (assuming there is a genuine effect, when there isn't) remains at 5%.

[21] AIC is a goodness of fit measure that is corrected for model complexity. It is used to compare different models and is not intrinsically interpretable (Field, 2013).

The data were visualised using standard scatter plots. $\delta^{13}C_{enamel}$ is compared with $\delta^{18}O_{enamel}$ in Chapter 5, and $\delta^{15}N_{collagen}$ is compared with $\delta^{13}C_{collagen}$ in Chapter 6. Where the current dataset is compared with archaeological datasets in Chapter 7, the contemporary $\delta^{13}C_{collagen}$ and $\delta^{13}C_{enamel}$ are adjusted by 2‰ to account for the fossil fuel effect (as explained in Chapter 2). For example, a value of -9.9‰ for a modern specimen is corrected to -7.9‰ where modern and archaeological values are being compared.

4.6 Summary

This chapter outlined the sample collection protocol, providing details of the fauna sampled. The laboratory sampling techniques for both bone and tooth enamel were described. The preparation of bone collagen and enamel apatite were explained, as well as the procedures used to measure isotope ratios on the mass spectrometer. The chapter also outlined methods for establishing the integrity of the data. The results are reported in the following chapters.

Chapter 5: Enamel apatite
$\delta^{13}C_{enamel}$ and $\delta^{18}O_{enamel}$

5.1 Introduction

This chapter presents $\delta^{13}C_{enamel}$ and $\delta^{18}O_{enamel}$ values for 476 animals (24 ungulate species, 2 primate species, and 11 carnivore species). Samples originated from all South African biomes that regularly receive rain in the winter months, as well as adjacent areas included for comparative purposes. As outlined in Chapter 3, these biomes incorporate significant environmental gradients. $\delta^{13}C_{enamel}$ and $\delta^{18}O_{enamel}$ is measured in different teeth along the tooth row in order to assess within-individual variation. Next, I present data for different groups of fauna from different biomes. C and O are considered in turn, and correlations are made between isotope values and climatic indices.

5.2 Tooth row analysis: Inter-tooth variability

The reason for analysing different teeth along the tooth row is to ascertain whether the choice of tooth for analysis influences the results. For this study, bulk enamel samples were taken from different teeth (P3, P4, M1, M2 and/or M3, as available) from each individual. The question was whether the isotopic values for any of the teeth showed systematic offsets from each other or from the median for that animal.

5.2.1 Carbon

The 36 ungulates from which multiple teeth were sampled showed ranges of intra-individual variation in $\delta^{13}C$ of 0.2-6.0‰ (Table 5.1, Figure 5.1). Excluding one bushpig with variation of 6.0‰ along the tooth row, the range was 0.2-4.9‰. Interpretation of small differences in delta values is difficult. Given that the standard deviation of repeated determinations of $\delta^{13}C$ in homogeneous carbonate materials is about 0.2‰, ranges of less than 1‰ were not regarded as indicating differences in diet. Zazzo *et al.* (2002) reported ranges of about 2.5‰ in $\delta^{13}C_{enamel}$ for intra-individual and inter-individual (intra population) variations in archaeological bovid teeth from Afghanistan. Wang *et al.* (2008) reported inter-tooth ranges of 0.7-3.1‰ for horses, 0.6-4.4‰ for goats and 1.4-4.8‰ for yaks. Ranges were attributed to differences in the $\delta^{13}C$ values of plants consumed during the time these teeth were mineralising. Of the 32 ungulates (excluding the one bushpig) in this study, seven had intra-individual ranges of less than 1‰, a further eight had ranges of less than 2‰, a further nine had ranges of less than 3‰ and the final 11 had ranges of less than 5‰ (Table 5.1).

Table 5. 1 $\delta^{13}C$ (‰) along the tooth row for individual animals. Table gives values for each tooth, the mean, median and range along the tooth row for each specimen.

Species	Common name	UCT #	Canine	P2	P3	P4	M1	M2	M3	Mean	Median	Range
Antidorcas marsupialis	Springbok	8080			-11.3	-11.8	-10.4	-10.6	-10.2	-10.9	-10.7	1.7
Antidorcas marsupialis	Springbok	8082			-9.2	-10.2	-12.1	-12.5	-10.3	-10.9	-10.6	3.3
Antidorcas marsupialis	Springbok	8085			-12.3	-13.0	-12.7	-13.0	-10.0	-12.2	-12.5	3.0
Antidorcas marsupialis	Springbok	8086			-15.5	-15.2	-13.1	-11.1	-12.5	-13.5	-13.3	4.4
Antidorcas marsupialis	Springbok	8087			-11.4	-11.0	-13.7	-11.6	-10.8	-11.7	-11.5	2.9
Antidorcas marsupialis	Springbok	8090			-11.1	-11.4	-11.1	-10.5	-11.4	-11.1	-11.1	1.0
Antidorcas marsupialis	Springbok	8098					-13.4	-13.1		-13.2	-13.2	0.2
Antidorcas marsupialis	Springbok	8101						-10.0	-10.7	-10.4	-10.4	0.7
Antidorcas marsupialis	Springbok	8104			-15.2	-14.6	-13.8	-11.3	-11.5	-13.3	-13.5	3.9
Cephalophus monticola	Blue duiker	1667			-13.7	-14.2	-15.8	-14.1	-13.2	-14.2	-14.1	2.6
Oryx gazella	Gemsbok	16386						-11.3	-8.7	-10.0	-10.0	2.6
Oryx gazella	Gemsbok	16387					-3.9	-5.4	-3.3	-4.2	-4.0	2.2
Oryx gazella	Gemsbok	16388					-7.6	-7.6	-9.2	-8.1	-7.9	1.6
Oryx gazella	Gemsbok	16389					-5.1	-2.8	-7.6	-5.2	-5.2	4.8
Oryx gazella	Gemsbok	16390					-11.0	-12.9		-12.0	-12.0	1.9
Oryx gazella	Gemsbok	16391					-12.9	-11.9		-12.4	-12.4	1.0
Oryx gazella	Gemsbok	16392					-5.9	-8.3	-9.5	-7.9	-8.1	3.6
Oryx gazella	Gemsbok	16393					-3.3	-8.2	-4.9	-5.5	-5.2	4.9
Oryx gazella	Gemsbok	16394					-12.6	-14.2		-13.4	-13.4	1.5
Oryx gazella	Gemsbok	16395					-11.9	-12.3		-12.1	-12.1	0.4
Potamochoerus larvatus	bushpig	1670		-14.3	-13.8	-14.0	-14.2	-14.0	-14.1	-14.1	-14.1	0.5
Potamochoerus larvatus	bushpig	14137			-11.6	-8.8	-5.6	-10.1	-8.6	-8.9	-8.9	6.0
Potamochoerus larvatus	bushpig	15348						-15.5	-14.7	-15.1	-15.1	0.7
Raphicerus campestris	steenbok	1074			-13.3	-13.2	-15.7	-12.9	-13.1	-13.6	-13.2	2.7
Raphicerus campestris	steenbok	2066		-12.9	-12.4	-12.9	-14.3	-13.4	-13.4	-13.2	-13.2	2.0
Raphicerus campestris	steenbok	2067				-15.1	-13.9	-11.0		-13.4	-13.6	4.1
Raphicerus campestris	steenbok	2073			-12.1	-11.4	-13.2	-9.5	-9.6	-11.2	-11.3	3.8
Raphicerus campestris	steenbok	2130			-9.3	-7.9	-12.0	-9.7	-10.7	-9.9	-9.8	4.1
Raphicerus campestris	steenbok	4290					-11.1	-11.5	-8.4	-10.3	-10.7	3.2
Raphicerus melanotis	grysbok	2080					-15.1	-15.3	-14.1	-14.9	-15.0	1.2
Raphicerus melanotis	grysbok	2111					-15.4	-13.6	-13.3	-14.1	-13.8	2.1
Sylvicapra grimmia	common duiker	13958			-15.5	-16.3	-15.5	-17.2	-13.3	-15.6	-15.6	3.9
Sylvicapra grimmia	common duiker	16384					-15.9	-13.9	-13.7	-14.5	-14.2	2.2
Tragelaphus strepsiceros	kudu	1709				-11.1	-10.7	-10.4	-8.8	-10.3	-10.4	2.3
Tragelaphus strepsiceros	kudu	1710			-10.6	-11.0	-11.5	-10.0	-11.5	-10.9	-11.0	1.5
Tragelaphus strepsiceros	kudu	1711				-11.4	-11.2	-10.3	-11.8	-11.2	-11.2	1.5
Canis mesomelas	Black-backed jackal	1717	-13.4	-13.5	-13.7	-12.2	-13.9			-13.3	-13.4	1.7
Canis mesomelas	Black-backed jackal	1718	-7.5			-11.6	-10.3			-9.8	-10.0	4.1
Caracal caracal	Caracal	1719	-14.4				-14.8			-14.6	-14.6	0.4
Caracal caracal	Caracal	1720	-12.6			-12.3	-13.0			-12.6	-12.6	0.6

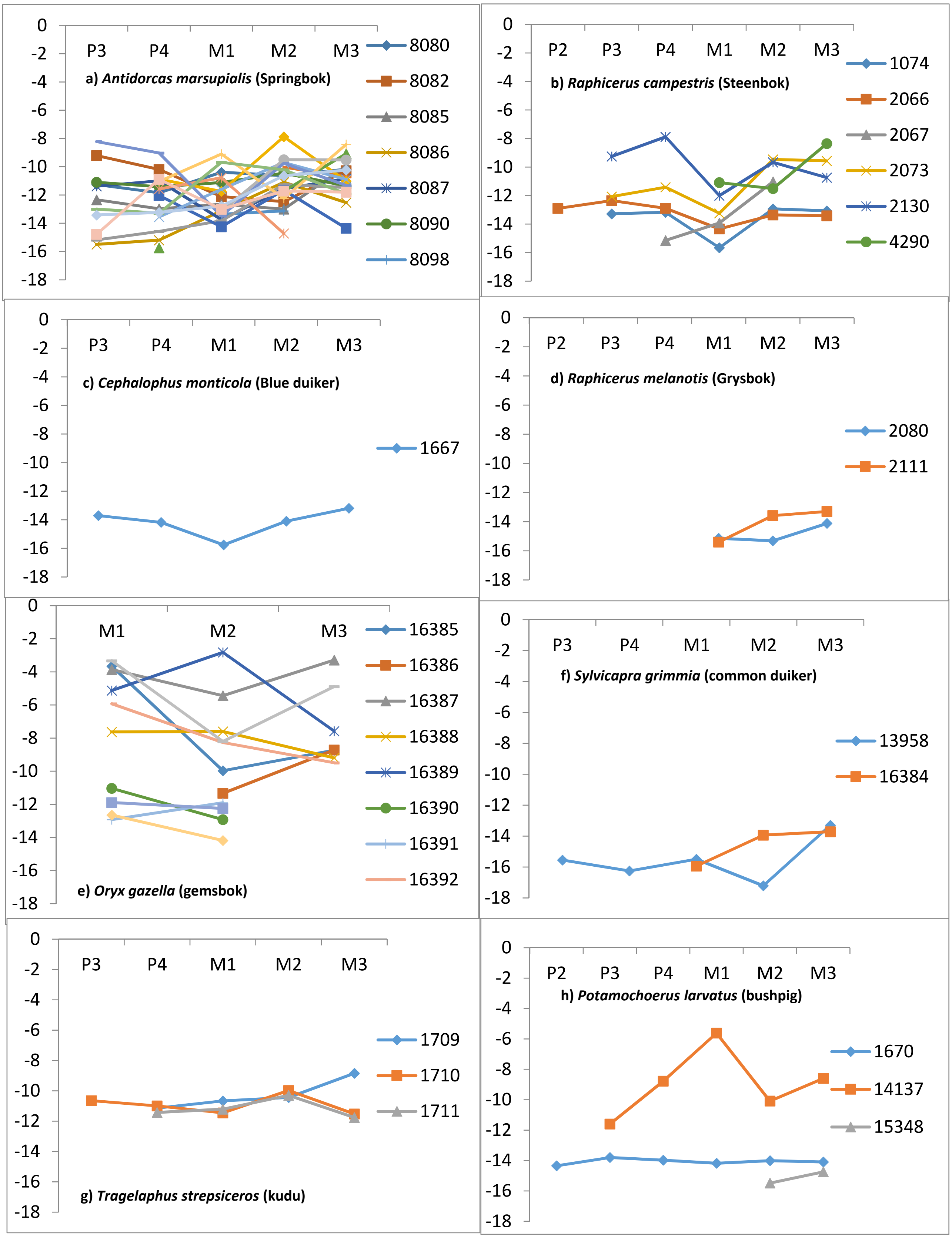

Figure 5. 1 $\delta^{13}C_{enamel}$ (‰) along the tooth row for a) springbok, b) steenbok c) blue duiker, d) grysbok, e) gemsbok, f) common duiker, g) kudu and h) bushpig. Each line represents a different individual (UCT sample identifier is listed in the legend).

In this study, there was no steady progression of δ^{13}C values from M1 to M2 to M3, as reported by Zazzo *et al.* (2002). Some M2s had values similar to M1s, but some were similar to M3s. Zazzo *et al.* (2002) found that the M1s of the archaeological bovids they measured were most depleted in ^{13}C, while the M2s were intermediate and the M3s variable. Since these authors analysed four to ten samples per tooth to assess intra-tooth variation, means and medians were calculated for comparison with values in this study. Zazzo *et al*. did not do any tests to establish the significance of differences. In this study, in *Oryx gazella* (gemsbok) (Figure 5.1e) the M3 and M2 were, in most cases, more negative than the M1. In eight out of the nine individuals for which an M1 was sampled, the M1 was more enriched in ^{13}C than the mean for the animal (range 0.1 to 2.1‰). In seven out of ten individuals, the M2 was more negative than the mean (range 0.2-2.7‰).

The M1s yielded the most negative δ^{13}C values of the three molars for *Cephalophus monticola* (blue duiker) (Figure 5.1c) and the two *Raphicerus* species (Figure 5.1b and d). It should be noted that there was no consistent progression of δ^{13}C values from M1s to M2s to M3s. In some individuals (2080 and 4290) the values for M1 and M2 were essentially identical; in others (1074, 2073, 2066 and 2111) the values for M2 and M3 were similar, or M2 was more enriched in ^{13}C. Mixed-feeders, especially *Antidorcas marsupialis* (springbok) (Figure 5.1a), did not show more inter-tooth variability (2.3±1.5‰) than species with greater diet specificity (for example *Raphicerus campestris* (steenbok) (3.3±0.9‰)). This would suggest that the browse/grass proportions in mixed-feeder diets (primarily C_3 browse in the case of springbok) may have remained relatively constant through time in the study area.

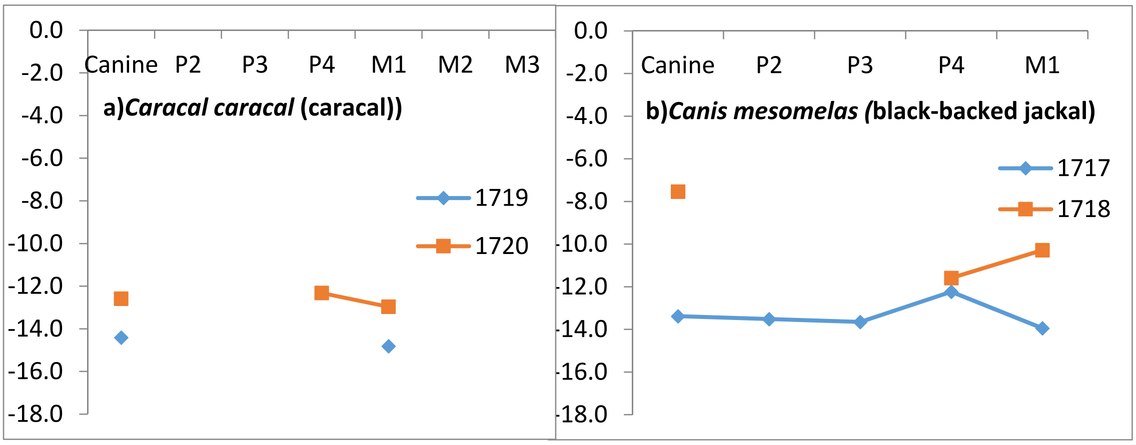

Figure 5. 2 δ^{13}C$_{enamel}$ (‰) along to tooth row for a) *Caracal caracal* and b) *Canis mesomelas*. Each line represents a different individual. UCT sample identifier is listed in the legend.

Two carnivore species were sampled along the tooth row. For two *Caracal caracal* (caracal) individuals (Figure 5.2a), only a canine and one or two other teeth were available for sampling. In both animals, values were similar along the tooth row, varying by less than 0.6‰ (Table 5.1). Of the *Canis mesomelas* (black-backed jackal) (Figure 5.2b), one showed an inter-tooth range of 4.1‰ while the range for the other animal was only 1.7‰. In both cases, the values for M1 provided a reasonable approximation of the mean for that animal.

5.2.2 Oxygen

The inter-tooth variation for most of the springbok individuals were relatively low (Figure 5.3) with all three molars less than 1‰ away from the mean (Table 5.2). Other than specimen 8086 which had the biggest change along the tooth row and specimen 8082 which had a relatively depleted M2, the M1s had similar $\delta^{18}O_{enamel}$ values as other molars. The blue duiker also had similar $\delta^{18}O_{enamel}$ values along the tooth row, with a total range of 2.2‰ (Figure 5.3c). Each of the three molars differed from the mean by <1‰. M1 was more negative than other molars. $\delta^{18}O_{enamel}$ for the gemsbok (Figure 5.3e) was also similar along the tooth row for most individuals; one showed a larger range (2.8‰ for 16393). In six out of the nine individuals with M1 and M2, the M1 was more enriched in ^{18}O than M2, while for three out of the five individuals with both M1 and M3, the M1 was more positive than M3. For two common duikers the values were relatively similar along the tooth rows (Figure 5.3f), with ranges of 0.8‰ for 16384 and 2.5‰ for 13958. In both cases, M1 was more negative than the mean and was also more negative than M2 and M3. M2 was the most representative of the mean. The three kudu individuals (Figure 5.3g) showed ranges of <1.0, 2.3 and 2.5‰. The M1 was consistently similar (not enriched or depleted) to the means or other molars. The M2 for these three specimens was the most representative of the mean. The ranges of $\delta^{18}O_{enamel}$ values for two bushpigs (Figure 5.3h) were low (0.6‰ for 14137 and 1.3‰ for 1670), while one showed a larger range (2.6‰ for 15348). For the two specimens with M1s, the values for M1 and M2 were similar and close to the mean for those specimens.

Table 5. 2 $\delta^{18}O_{enamel}$ (‰) along the tooth row for individual animals.

Species	Common name	UCT code	Canine	P2	P3	P4	M1	M2	M3	Mean	Median	Range
Antidorcas marsupialis	springbok	8080			4.2	4.6	4.7	4.3	4.8	4.5	4.6	0.5
Antidorcas marsupialis	springbok	8082			4	2.6	4.4	2.6	4.1	3.5	4.0	1.8
Antidorcas marsupialis	springbok	8085			5.8	5.4	4.1	4.5	5.7	5.1	5.4	1.7
Antidorcas marsupialis	springbok	8086			3.4	3.1	2.8	4.3	6.7	4.1	3.4	3.9
Antidorcas marsupialis	springbok	8087			5.4	5.3	4.1	4.3	5.8	5	5.3	1.8
Antidorcas marsupialis	springbok	8090			2.5	3.2	4.5	3.5	3.5	3.4	3.5	2
Antidorcas marsupialis	springbok	8098					6.1	6.3		6.2	6.2	0.2
Antidorcas marsupialis	springbok	8101						5.7	4.1	4.9	4.9	1.6
Antidorcas marsupialis	springbok	8104			4.7	5.7	4.7	5.5	5.9	5.3	5.5	1.2
Cephalophus monticola	blue duiker	1667			-6	-4.2	-4.9	-4.1	-3.8	-4.6	-4.2	2.2
Oryx gazella	gemsbok	16386						3.7	2.8	3.2	3.3	1
Oryx gazella	gemsbok	16387					4.6	4	4.2	4.3	4.2	0.6
Oryx gazella	gemsbok	16388					3.4	3	4.6	3.7	3.4	1.5
Oryx gazella	gemsbok	16389					3.1	2.5	1.4	2.3	2.5	1.7
Oryx gazella	gemsbok	16390					2.5	0.7		1.6	1.6	1.9
Oryx gazella	gemsbok	16391					2	2.4		2.2	2.2	0.4
Oryx gazella	gemsbok	16392					3.1	3.4	3.9	3.5	3.4	0.9
Oryx gazella	gemsbok	16393					4.5	2.7	1.6	2.9	2.7	2.8
Oryx gazella	gemsbok	16394					2.2	1.4		1.8	1.8	0.8
Oryx gazella	gemsbok	16395					1.3	1.5		1.4	1.4	0.3
Potamochoerus larvatus	bushpig	1670		-5	-4.7	-5	-5.4	-5.2	-4.1	-4.9	-5.0	1.3
Potamochoerus larvatus	bushpig	14137			-3.1	-2.6	-3.2	-3.2	-3.2	-3.1	-3.2	0.6
Potamochoerus larvatus	bushpig	15348						-6.4	-3.8	-5.1	-5.1	2.6
Raphicerus campestris	steenbok	1074			5.4	5.7	4.3	5	3.5	4.8	5.0	2.2
Raphicerus campestris	steenbok	2066		4.6	5.7	4.4	4.4	4.3	5.1	4.7	4.5	1.5
Raphicerus campestris	steenbok	2067				3.2	3.7	5.9		4.3	3.7	2.6
Raphicerus campestris	steenbok	2073			1.5	1.8	1.5	3	1.2	1.8	1.5	1.8
Raphicerus campestris	steenbok	2130			11.1	10.4	8	8.4	5.8	8.8	8.4	5.3
Raphicerus campestris	steenbok	4290					2.2	5.6	8.4	5.4	5.6	6.2
Raphicerus melanotis	grysbok	2080					-2.1	-3.4	-0.6	-2	-2.1	2.8
Raphicerus melanotis	grysbok	2111					1.3	3.7	1.8	2.3	1.8	2.5
Sylvicapra grimmia	common duiker	13958			-0.2	-0.2	-0.7	0.6	1.7	0.2	-0.2	2.5
Sylvicapra grimmia	common duiker	16384					1.8	2.1	2.5	2.1	2.1	0.8
Tragelaphus strepsiceros	kudu	1709				1.8	1.8	2.3	2.4	2.1	2.1	0.6
Tragelaphus strepsiceros	kudu	1710			2.4	2	1.9	1.3	-0.1	1.5	1.9	2.5
Tragelaphus strepsiceros	kudu	1711				1	3.1	2.2	0.8	1.8	1.6	2.3
Canis mesomelas	black-backed jackal	1717	-1.5	-1.9	-1.2	-1.4	-2			-1.6	-1.5	0.9
Canis mesomelas	Black-backed jackal	1718	-1.7			-2.8	-2.1			-2.2	-2.1	1.1
Caracal caracal	caracal	1719	-3.4				-3.3			-3.4	-3.4	0.2
Caracal caracal	caracal	1720	-2.3			-2.4	-2			-2.2	-2.3	0.4

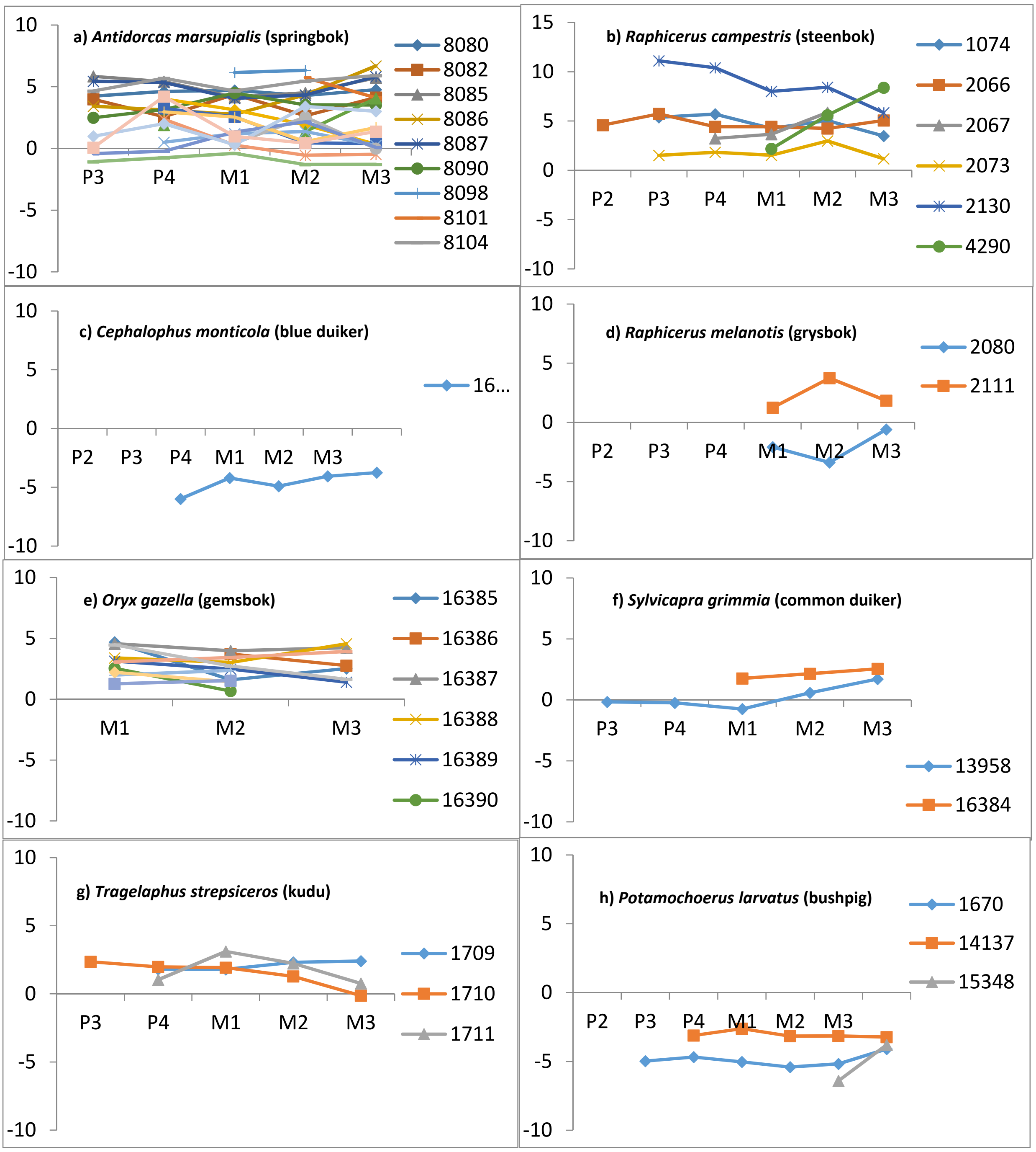

Figure 5. 3 $\delta^{18}O_{enamel}$ (‰) along the tooth row for a) springbok, b) steenbok, c) blue duiker, d) grysbok, e) gemsbok, f) common duiker, g) kudu and h) bushpig. Each line represents a different individual. UCT sample identifier is listed in the legend.

There were some large variations in $\delta^{18}O_{enamel}$ along the tooth row for steenbok (Figure 5.3b). Two specimens had large ranges (5.3‰ and 6.2‰), two had moderate ranges (2.2‰ and 2.6‰), and two had small ranges (<2‰). In most cases, M1 was more depleted in ^{18}O than the other molars and in all cases M1 was more negative than the mean. For *Raphicerus melanotis* (grysbok) (Figure 5.3d) the range of values for both specimens was <3‰. In both cases, M1 was more depleted in ^{18}O than the mean; however, M1 was more negative than M2 for 2111 and more positive than M2 for 2080. Murphy *et al.* (2007a) also found no consistent offset between the $\delta^{18}O$ of kangaroo molars. They concluded that this meant that the "weaning" signal is not evident or that the seasonal $\delta^{18}O$ of rainfall is overriding it (Murphy *et al*., 2007a).

Amongst carnivores, the caracal and the black-backed jackal showed small inter-tooth ranges of <1.1‰ for all four animals. Carnivores mature rapidly, and thus, their teeth mineralise and erupt much more quickly than in ungulates. There is perhaps also less variation due to the suckling effect because after being weaned, carnivores continue to consume animal tissue-based diets – the shift in the nature of the diet (effectively in trophic level) between pre- and post-weaning is less marked than for herbivores.

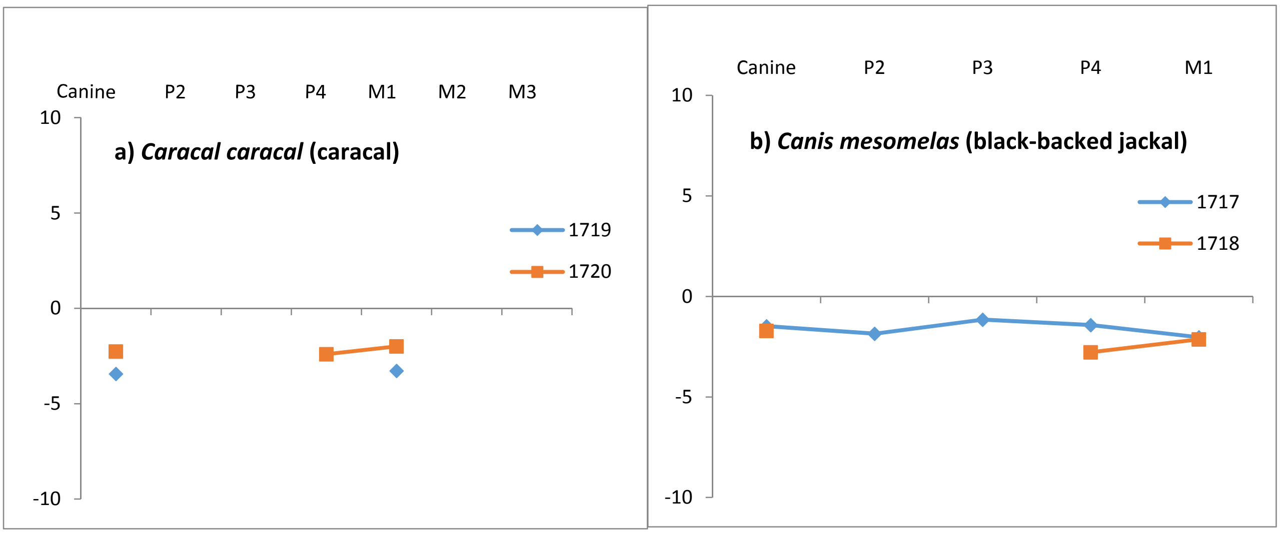

Figure 5. 4 $\delta^{18}O_{enamel}$ (‰) along to tooth row for a) *Caracal caracal* and b) *Canis mesomelas*. Each line represents a different individual. UCT sample identifier is listed in the legend.

In summary, there was variation in both $\delta^{13}C_{enamel}$ and $\delta^{18}O_{enamel}$ between teeth along the tooth row. The dataset did not show consistent offsets between any of the molars for either $\delta^{13}C_{enamel}$ or $\delta^{18}O_{enamel}$. Some species showed less variation (e.g. springbok, gemsbok) than others (e.g. steenbok). Based on these results, there is no reason to believe that choosing any particular tooth for analysis is likely to produce a dataset which is more reflective of the animal as a whole. Based on the samples available for analysis, carnivorous species showed less variation along the tooth row than ungulate species.

5.3 $\delta^{13}C_{enamel}$

5.3.1 General observations

$\delta^{13}C_{enamel}$ values in this study ranged between -18.9‰ and +2.0‰. All values are listed in Appendix 7. Where more than one tooth was sampled, averages were reported for that individual. As the data were not normally distributed, non-parametric approaches were used. Means and standard deviations are listed in Appendix 8a, for comparison with other studies in which data were summarised in this way.

Ungulates (the largest group) had $\delta^{13}C_{enamel}$ values ranging from -18.9‰ to 2.0‰ (median = -10.9‰, n = 297). Values for carnivores ranged between -18.2‰ and -4.9‰ (median = -12.6‰, n = 33). The $\delta^{13}C_{enamel}$ values of primates ranged between -17.1‰ and -5.2‰ (median of -14.5‰, n = 146). Table 5.3 provides summary statistics for each grouping for all biomes combined.

Table 5. 3 Descriptive statistics for $\delta^{13}C_{enamel}$ (‰) by faunal category.

Type	Feeder type	N	Median	Minimum	Maximum
Carnivore	Carnivore	33	-12.6	-18.2	-4.9
Primate	Omnivore	146	-14.5	-17.1	-5.2
Ungulate		297	-10.9	-18.9	2.0
	Browser	121	-13.5	-18.9	-7.3
	Grazer	121	-3.2	-14.2	2.0
	Mixed feeder	41	-11.7	-16.6	-7.0
	Omnivore	14	-14.8	-17.5	-8.9

Grazers had the biggest range in $\delta^{13}C$ (Figure 5.5), reflecting consumption of varying amounts of C_4 grasses. Both omnivores and carnivores had relatively negative $\delta^{13}C$ values.

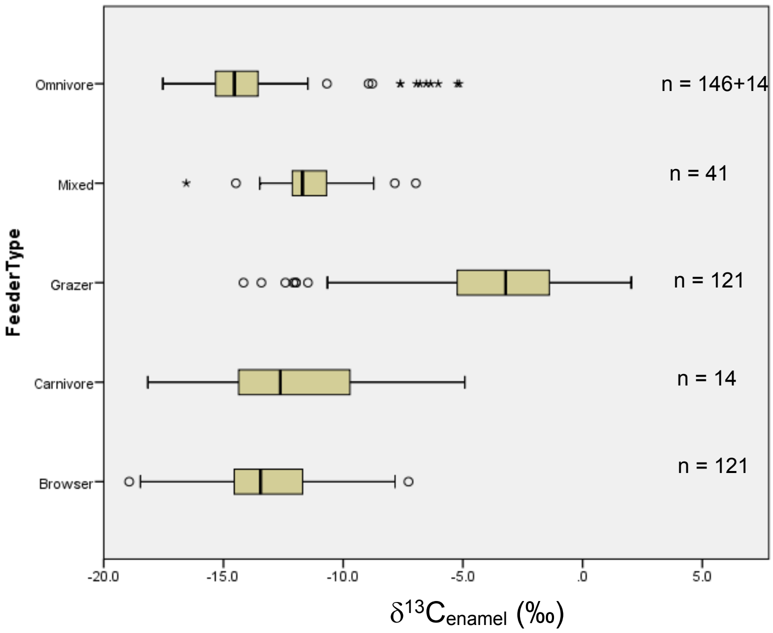

Figure 5. 5 $\delta^{13}C_{enamel}$ (‰) for all biomes by feeder type. Omnivores include primates (n=146) and omnivorous ungulates (n=14). Bold vertical lines indicate the median, with surrounding boxes representing the interquartile range (first quartile to third quartile). The whiskers indicate the range of values that are not outliers. Outliers (values between 1.5 and 3 times the interquartile range away from the median) are indicated by open circles and extreme outliers (values more than 3 times the interquartile range away from the median) are indicated by stars.

5.3.1 By feeding preference

5.3.1.1 Ungulates

The $\delta^{13}C$ values observed in tooth enamel of browsers varied according to vegetation type (Figure 5.6a) (Kruskal-Wallis H (5) = 30.66, $p < 0.000$). The most positive $\delta^{13}C$ values occurred in the Nama Karoo (median = -10.8‰, n = 7) and in the Albany Thicket biomes (median = -12.0‰, n = 22). The most negative $\delta^{13}C_{enamel}$ values (median = -15.4‰, n =11) occurred in the Forest biome. $\delta^{13}C_{enamel}$ values from the Forest biome were significantly different from the Savanna (pairwise comparison with adjusted *p*-values, $p = 0.002$), Nama Karoo ($p < 0.000$) and Albany Thicket biomes ($p < 0.000$). $\delta^{13}C_{enamel}$ values from the Fynbos and Succulent Karoo biomes, the two cooler winter rainfall biomes, were both negative (medians = -14.2‰ and -13.6‰, respectively) and were not significantly different (p = 0.140). Fynbos and Nama Karoo biomes were significantly different (p = 0.030).

Figure 5.6a also illustrates that biomes with the highest proportions of winter rainfall (Succulent Karoo, Fynbos and Forest) had the smallest spread of $\delta^{13}C_{enamel}$ values around the medians (1.6‰, 3.7‰ and 2.9‰ respectively). The biomes with more summer rainfall (Savanna, Nama Karoo and Albany Thicket) had the widest spreads of data around the medians (ranges of 6.0‰, 4.6‰ and 7.3‰ respectively) and the most positive $\delta^{13}C_{enamel}$ values, suggesting that browsing species do in fact consume small amounts of grass, including C_4 grass where available, and/or CAM plants. The range for browsers from the Albany Thicket biome was larger than that of the Fynbos biome. Figure 5.7a shows the most negative values (shown as green circles) to be in the west of the country, where winter rainfall is strongest.

$\delta^{13}C_{enamel}$ of grazing species varied significantly across biomes (Kruskal-Wallis H (4) = 23.72, $p < 0.001$), likely reflecting differences in the proportions of C_3 and C_4 grasses consumed (Figure 5.6b). Figure 5.6b shows that among grazers, $\delta^{13}C_{enamel}$ values from the Fynbos biome were the most negative (median=-7.7‰), along with the Succulent Karoo biome (median=-5.2‰). Pairwise comparisons with adjusted *p*-values showed no significant difference in $\delta^{13}C_{enamel}$ between these two biomes ($p = 0.154$), although the sample size for the Fynbos biome was small. Biomes where summer rain is experienced had more positive $\delta^{13}C_{enamel}$ values (Albany Thicket, Nama Karoo and Savanna). There were significant differences between the Succulent Karoo and two of the summer rainfall biomes: Albany Thicket biome ($p < 0.001$) and the Savanna biome ($p = 0.001$). No tooth enamel could be obtained from grazers from the Forest biome, so that biome was excluded here. Figure 5.7b illustrates the geographical patterning in $\delta^{13}C_{enamel}$ of grazers. Values in the east and north were least negative, while in the Fynbos biome to the south $\delta^{13}C_{enamel}$ values were most negative. More positive $\delta^{13}C$ values were found in areas with greater abundance of C_4 grass.

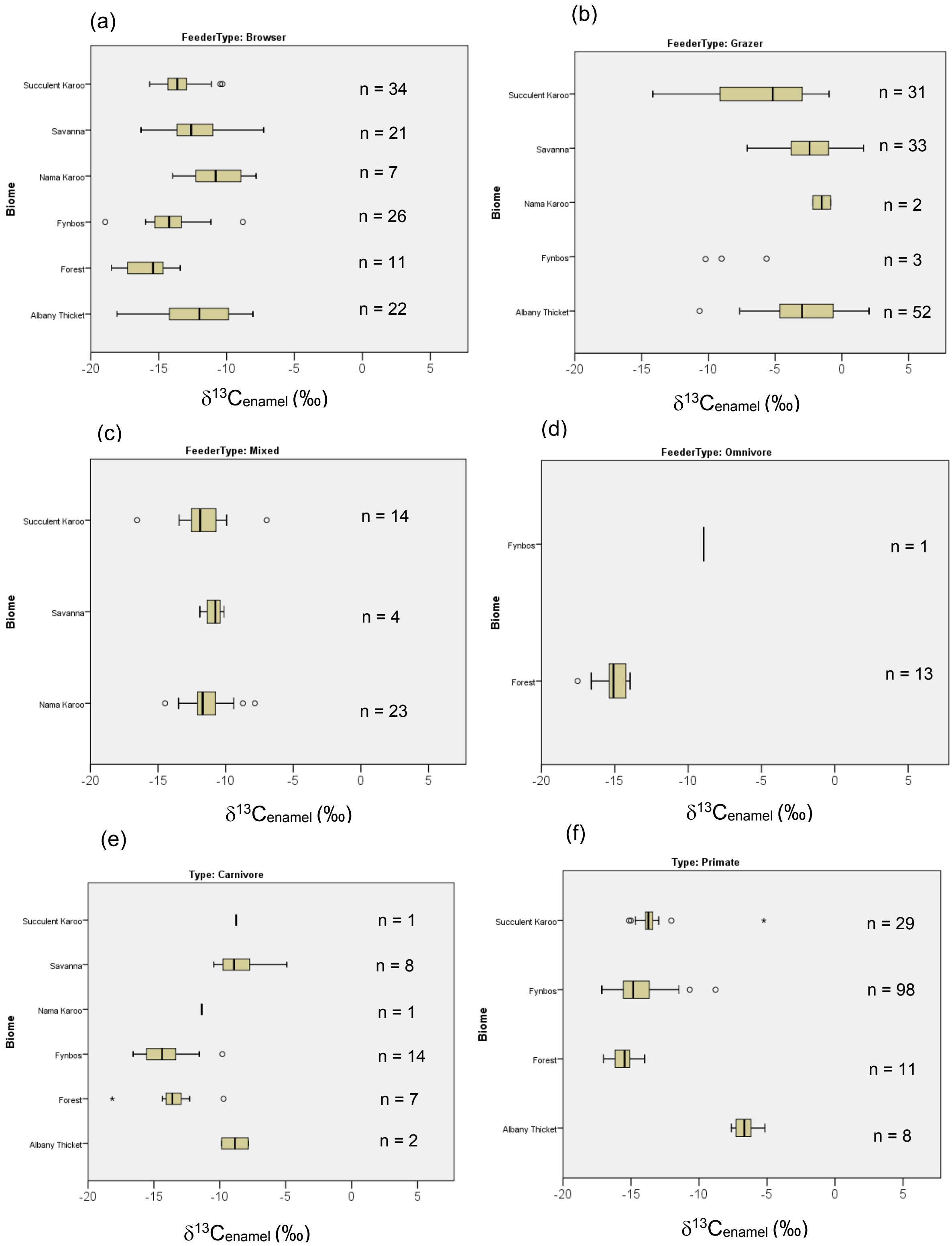

Figure 5. 6 δ^{13}Cenamel (‰) of a) browsers, b) grazers, c) mixed feeders, d) omnivorous ungulates, e) carnivores and f) primates. See legend to Fig. 5.5 for an explanation of the format of the plots.

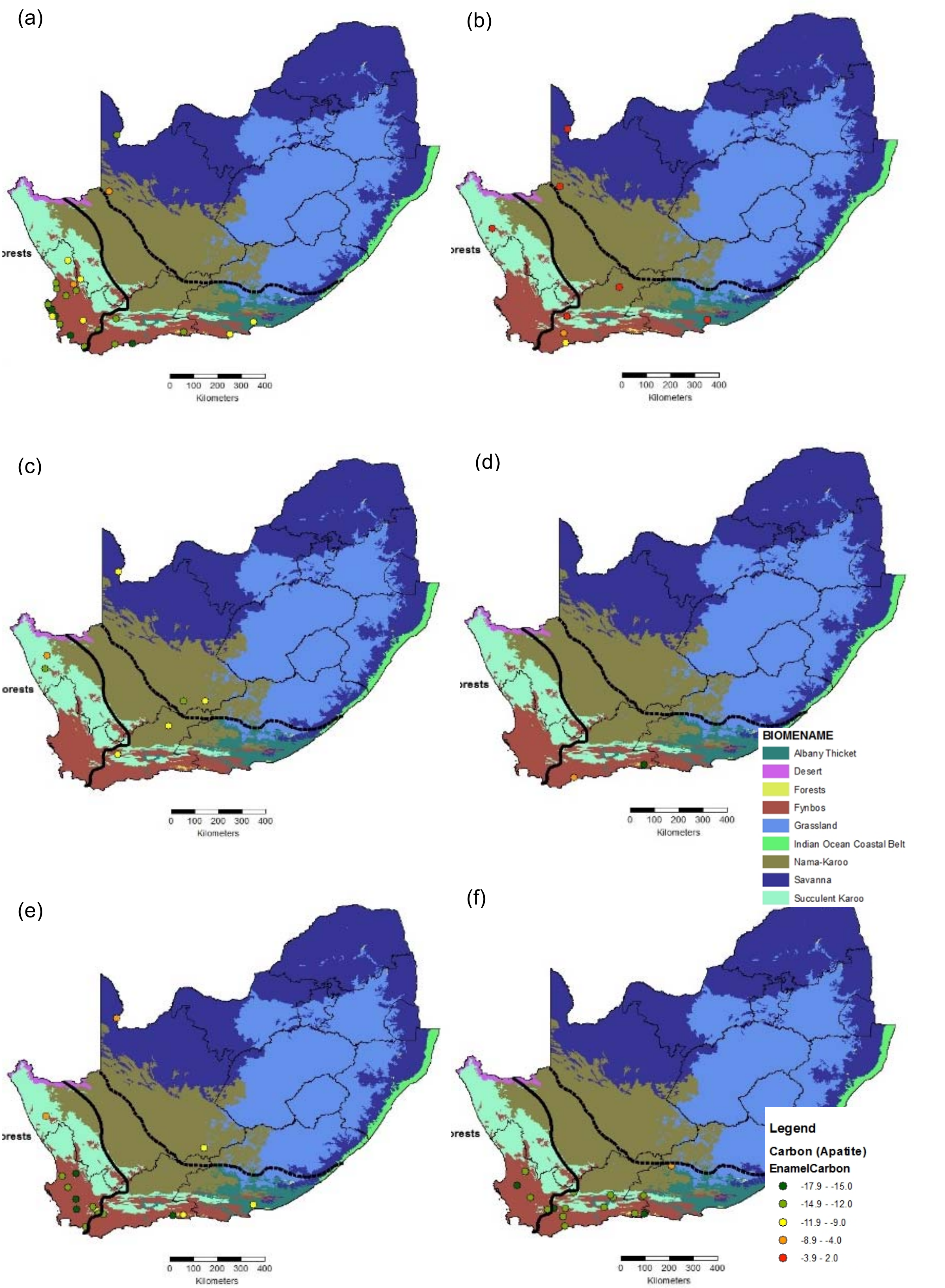

Figure 5. 7 $\delta^{13}C_{enamel}$ (‰) of a) browsers, b) grazers, c) mixed feeders, d) omnivorous ungulates, e) carnivores and f) primates by collection location across the sampled biomes. Circles represent means per collection location. The solid line indicates the approximate extent of the winter rainfall zone, the dotted line indicates the beginning of the summer rainfall zone and the area between the lines indicates the year-round rainfall zone.

This study included only a small number of mixed feeders, all springbok. The largest number of samples derived from the Nama Karoo (n = 23) where values ranged from -14.5‰ to -7.8‰ with a median of -11.7‰ (Figure 5.6c). These values were similar to those from the Succulent Karoo (n = 14) where the median was -11.9‰. Four animals derived from the Savanna biome, with a median of -10.8‰ (Figure 5.7c). A Kruskal-Wallis test did not show significant differences across biomes in this data set (Kruskal-Wallis H (4) = 1.315, $p = 0.518$). Excluding the outliers, the range of $\delta^{13}C_{enamel}$ was small (-13.5‰ to -9.5‰).

Omnivorous ungulates (all bushpigs) were collected from only two biomes: Fynbos (n = 1) and Forest (n = 13) (Figures 5.6d and 5.7d). The values for animals from the forest biome were consistently negative (-17.5‰ to -14.0‰) and fell within the range of browser values for this biome. The single specimen from the Fynbos biome was more positive at -8.9‰.

5.3.1.2 Carnivores

Carnivores from the different biomes showed significantly different $\delta^{13}C_{enamel}$ values (Kruskal-Wallis H (5) = 20.35, $p = 0.001$). Those from the Fynbos biome had the lowest values (median = -14.4‰). The Forest biome, which also receives some rain in the winter, was also low (median -13.6‰). Nama Karoo had only one sample (-11.4‰). Albany Thicket and Savanna were the least depleted in ^{13}C at -8.8‰ and -8.5‰ respectively (Figure 5.7e). The Fynbos and Savanna biomes were significantly different from each other ($p = 0.001$). There were no significant differences between the other biomes.

The map in Figure 5.7e illustrates the distinction between the winter rainfall Fynbos biome and the other summer rainfall, hotter biomes – Savanna, Nama Karoo and Albany Thicket.

5.3.1.3 Primates

Primates from the Albany Thicket had less negative values (median -6.7‰, n = 8) than those from other biomes (Figure 5.7f). The more positive values indicate that primates in the Albany Thicket are eating more ^{13}C enriched foods. Baboons are known to be fond of the fruits of the prickly pear (*Opuntia* sp.) which is abundant in this region, a likely contributor to more positive $\delta^{13}C$ values. Other CAM foods may also be important. The Forest, Fynbos and Succulent Karoo biomes (all three of which receive a significant proportion of their rain in the winter months) had more negative medians of -15.5‰, -14.8‰ and -13.7‰ respectively. These negative values indicate the consumption of mainly C_3 resources in these biomes. Values from Albany Thicket were significantly different from Fynbos ($p < 0.000$), Forest ($p < 0.000$) and Succulent Karoo biomes ($p = 0.010$). Interestingly, the Succulent Karoo biome was also significantly different from the Forest ($p < 0.000$) and Fynbos biomes ($p = 0.001$). Ambrose and DeNiro (1986a) found the $\delta^{13}C_{collagen}$ values of East African baboons (*Papio* *anubis)* to range between -19.6‰ and -15.3‰, which in a summer rainfall zone such as East Africa indicates a predominantly C_3 plant diet. This range is similar to that found in the Succulent Karoo, Fynbos and Forest biomes in the current data set.

5.3.2 By biome

This section describes the same $\delta^{13}C_{enamel}$ data separated by biome. In this context, the ungulate and primate omnivores are analysed as a single group.

In the Forest biome, browsers and omnivores showed median $\delta^{13}C_{enamel}$ values of -15.4‰ and -15.2‰ respectively. Values for these two groups were not significantly different. The Forest biome, being moister and cooler relative to other biomes, had the most negative values (Figure 5.8a). In this environment, grazers are scarce, therefore no results were available for grazing species. Carnivore $\delta^{13}C$ was slightly less negative than for browsers (median -13.6‰, n = 24) although still at the C_3 end of the spectrum. $\delta^{13}C$ values for carnivores were significantly different from browsers ($p < 0.050$) but not from omnivores ($p = 0.116$).

In the Fynbos biome, the median $\delta^{13}C_{enamel}$ value for browsers was -14.2‰. Although only three grazers were sampled from this biome, Figure 5.8b illustrates that their enamel was more enriched in ^{13}C, with a median of -7.7‰. $\delta^{13}C_{enamel}$ values for carnivores and omnivores were similar to browsers, with medians of -14.4‰ and -14.8‰ respectively. Pairwise comparisons with adjusted *p*-values indicated that there were significant differences between grazers and the other three animal types: browsers ($p = 0.001$); carnivores ($p < 0.000$) and omnivores ($p < 0.000$). Carnivores, browsers and omnivores were not significantly different from each other (omnivore: carnivore $p = 0.241$; omnivore: browser $p = 0.200$; carnivore: browser $p = 0.953$).

For the Succulent Karoo (Figure 5.8c), median $\delta^{13}C_{enamel}$ for browsers was -13.6‰ (n = 34), while for grazers it was -5.2‰ (n = 31). These were significantly different ($p < 0.000$). The values for grazers were varied, but the median was less negative than expected since this is a winter rainfall biome. The grazing species included gemsbok, red hartebeest and two zebra species. Of the grazers, the largest number (n = 23) were gemsbok, which exhibited the largest range of $\delta^{13}C$ values as well as the most negative values. All the gemsbok were collected from the Anysberg Nature Reserve, on the boundary of the Succulent Karoo and the Fynbos biomes. Individuals fell into two distinct groups: one with a median of -12.2‰ (n = 8) and the other with a median of -4.5‰ (n = 15). The two groups identified based on the $\delta^{13}C_{enamel}$ values were reported to the game ranger. He explained that when Anysberg was bought by the WWF in 2000, they obtained gemsbok from two nearby farms (Touwsfontein and Skerpkrans). Although both lie within the Succulent Karoo, these two farms probably obtained their gemsbok from different places in South Africa. The mandibles from the less negative group all had M3s present while the M3s had not yet erupted in the more negative group. This indicates that the more positive group contained older animals that came from the neighbouring farms (and from somewhere else prior to that) and that the more negative group contained those younger animals born in Anysberg. Adults should also have broader dietary niches possibly contributing to the different $\delta^{13}C_{enamel}$ values.

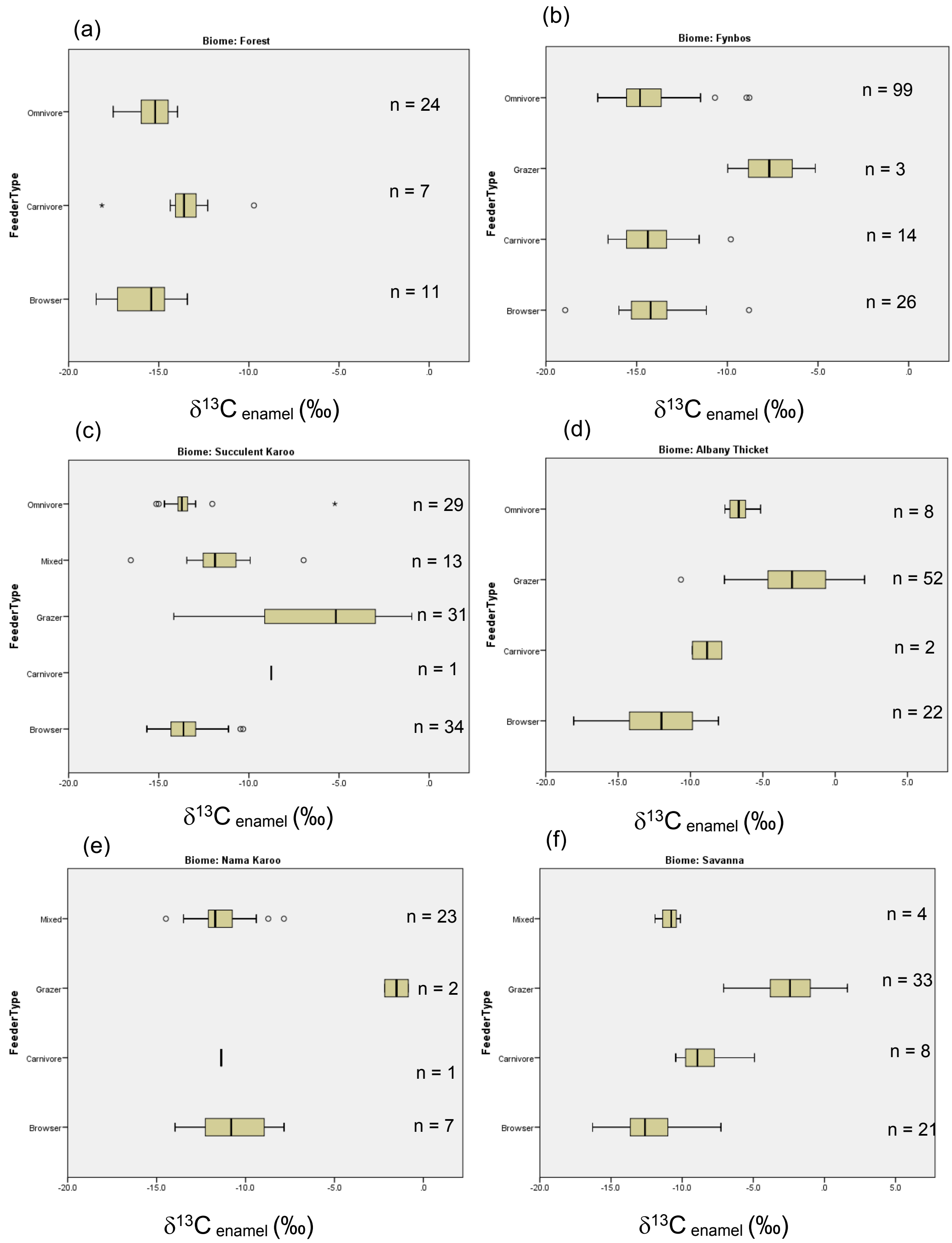

Figure 5. 8 $\delta^{13}C_{enamel}$ (‰) for the a) Forest, b) Fynbos, c), Succulent Karoo, d) Albany Thicket, e) Nama Karoo and f) Savanna biomes by feeder type. See legend to Fig. 5.5 for an explanation of the format of the plots.

The mixed feeders were also significantly different from both the omnivores (p = 0.027) and the browsers (p = 0.043).

In the Albany Thicket biome, $\delta^{13}C_{enamel}$ median for browsers was -12.0‰ (n = 22), while for grazers it was -3.0‰ (n = 52). The ranges of values for browsers and grazers did not overlap, apart from one outlier (p < 0.000). Carnivores (median = -8.8‰, n = 2) and omnivores (median = -6.7‰, n = 8) consumed both C_3 and C_4 food items (Figure 5.8d).

Browsers from the Nama Karoo had median $\delta^{13}C_{enamel}$ of -10.8‰ (n = 7), while the value for two grazers was -1.5‰. Mixed feeders (springbok) had $\delta^{13}C_{enamel}$ values similar to those of browsers and were likely to have eaten mainly browse (Figure 5.8e).

Browsers in the Savanna biome had a median $\delta^{13}C$ value of -12.6‰ (n = 21). The grazers had a median of -2.4‰ (n = 33) Figure 5.8f illustrates this distinction between grazing and browsing species (p < 0.001). Mixed feeders fell between the grazers and browsers. They were not significantly different from browsers (p = 0.581), but they were significantly different from grazers (p = 0.012), indicating they were eating more leaves than grass (Kruskal-Wallis H (3) = 51.86, p < 0.000). Carnivores were significantly different from grazers (p = 0.022) but not from browsers (p = 0.344).

In general, the expected patterns for biomes that receive significant summer rainfall were that $\delta^{13}C$ values for grazers are more positive (falling towards the C_4 end of the spectrum) and values for browsers are more negative (as expected for C_3 feeders). In winter rainfall biomes the grazers were more negative which was expected since they consume mainly C_3 grass in these areas. Although browsers displayed C_3 values, the medians differed across biomes, indicating that environmental factors and/or slight variations in diet were playing a role in determining the $\delta^{13}C_{enamel}$ values. In most animal groups, the Forest biome yielded the most negative values with the Fynbos biome also low, but not to the same degree.

5.3.3 Relationships between $\delta^{13}C_{enamel}$ and meteorological factors

The relationships between $\delta^{13}C_{enamel}$ and meteorological factors were investigated in the following sections. First correlations are run and then regression models were constructed, which were used to predict the $\delta^{13}C_{enamel}$ based on a set of meteorological factors.

5.3.3.1 Correlations

Despite comparatively small numbers, carnivores demonstrated the closest correlations between $\delta^{13}C_{enamel}$ and various meteorological factors, with significant correlations with eight out of nine factors (p <0.01) (Table 5.4). The only factor that did not show a significant correlation was SAI. Omnivores also had a high correlation rate, with seven out of nine factors being significantly correlated (p <0.05). Browsers showed significant correlations with seven meteorological factors, grazers with only three (MAT, SAI and WCR, all with p <0.01). Only browsers showed a significant correlation with MAP. Mixed feeders did not show significant correlations with any of the meteorological factors.

Table 5. 4 Correlation coefficients for $\delta^{13}C_{enamel}$ and meteorological variables from all locations. The number of specimens varies across the rows because not all variables are available for all locations. 'Omnivore' includes ungulate omnivores and primate omnivores. Correlation coefficients are considered significant when *p* <0.05 (in bold). Mean annual precipitation (MAP), mean annual temperature (MAT), mean annual soil moisture stress (MASMS), mean annual potential evapotranspiration (MAPE), relative humidity (RH), summer aridity index (SAI), winter concentration of rainfall (WCR), moisture index (MI) and water deficit (WD).

FeederType		MAP	MAT	MASMS	MAPE	RH	SAI	WCR	WD	MI
Browser	Correlation Coefficient (r_s)	**-0.365****	**0.319****	**0.278****	**0.325****	-0.174	0.145	**-0.419****	**0.329****	**-0.350****
	p (2-tailed)	<0.001	<0.001	0.003	<0.001	0.056	0.113	<0.001	<0.001	<0.001
	N	121	121	110	121	121	121	121	121	121
Grazer	Correlation Coefficient (r_s)	-0.046	**0.399****	0.046	0.043	0.018	**0.403****	**-0.380****	0.043	-0.046
	p (2-tailed)	0.618	<0.001	0.619	0.642	0.845	<0.001	<0.001	0.643	0.618
	N	121	121	121	121	121	121	121	121	121
Mixed	Correlation Coefficient (r_s)	-0.131	0.036	0.162	0.182	-0.162	0.162	-0.117	0.160	-0.131
	p (2-tailed)	0.413	0.825	0.310	0.255	0.311	0.311	0.466	0.317	0.413
	N	41	41	41	41	41	41	41	41	41
Omnivore	Correlation Coefficient (r_s)	**-0.402****	-0.015	**0.585****	**0.465****	**-0.168***	0.066	**-0.467****	**0.511****	**-0.480****
	p (2-tailed)	<0.001	0.847	<0.001	<0.001	0.034	0.404	<0.001	<0.001	<0.001
	N	160	160	136	160	160	160	160	160	160
Carnivore	Correlation Coefficient (r_s)	**-0.662****	**0.683****	**0.793****	**0.620****	**-0.547****	0.143	**-0.570****	**0.620****	**-0.589****
	p (2-tailed)	<0.001	<0.001	<0.001	<0.001	0.001	0.428	0.001	<0.001	<0.001
	N	33	33	26	33	33	33	33	33	33

**. Correlation is significant at the 0.01 level (2-tailed).

*. Correlation is significant at the 0.05 level (2-tailed).

Following this test, regression models were constructed, which were used to predict the meteorological factors from the isotope values.

5.3.3.2 Simple regression

For ungulates, regressions of $\delta^{13}C_{enamel}$ against MAT, SAI and WCR were significant (Table 5.5). Detailed outcomes of each model run per meteorological factor can be found in Appendix 9. In order to interpret these results better, one needs to take into consideration the range in values for each of the meteorological factors. The reason for this is that the unstandardised regression coefficient (B value) is the change in $\delta^{13}C_{enamel}$ per one unit change in the meteorological factor. Since many meteorological factors have much larger or smaller ranges than one, it is more sensible to adjust to an appropriate scale for each factor. For example, it would be suitable to refer to a change of 100 mm for MAP. Thus, Table 5.6 outlines how each meteorological factor will be discussed.

Table 5. 5 Summary outcome of regression models for $\delta^{13}C_{enamel}$ for ungulates against each meteorological factor individually. The adjusted r^2 is modified for the number of predictors in the model. For models with only one predictor, r^2 should suffice, but for consistency r^2 adjusted is reported. B is the unstandardised regression coefficient (the change in the isotope value with a one unit change in meteorological factor); t is the test statistic (used to test whether B is significantly different from zero). *p*-values that are significant at <0.05 are in bold. Mean annual precipitation (MAP), mean annual temperature (MAT), mean annual soil moisture stress (MASMS), mean annual potential evapotranspiration (MAPE), relative humidity (RH), summer aridity index (SAI), winter concentration of rainfall (WCR), moisture index (MI) and water deficit (WD).

					95% Confidence interval			
Met factors	B	Std. error	t	*p*	Lower bound	Upper bound	r^2	r^2 adj
MAP	-0.001	0.001	-1.089	0.277	-0.003	0.001	0.74	0.73
MAT	0.876	0.218	4.014	**<0.001**	0.446	1.306	0.75	0.75
MASMS	0.059	0.044	1.323	0.187	-0.029	0.146	0.72	0.71
MAPE	0.001	0.000	1.257	0.210	0.000	0.002	0.74	0.73
RH	0.001	0.015	0.049	0.961	-0.030	0.031	0.74	0.73
SAI	0.012	0.003	4.663	**<0.001**	0.007	0.017	0.76	0.75
WCR	-0.023	0.009	-2.437	**0.015**	-0.041	-0.004	0.74	0.74
WD	0.000	0.000	1.250	0.212	0.000	0.001	0.74	0.73
MI	-2.922	1.732	-1.687	0.093	-6.332	0.487	0.74	0.74

Table 5. 6 Adjustments to be made to each meteorological factor (*MI is MAP/MAPE, both of which are measured in mm).

Met factors	Minimum	Maximum	Range	Changes in $\delta^{13}C_{enamel}$ in reference to	Thus B value adjusted by
MAP	105mm	863	**758**	100 mm	X 100
MAT	14°C	19	**4.30**	1 degree C	no change
MASMS	64%	86%	**22%**	10%	divided by 10
MAPE	1647mm	2919	**1272**	100 mm	X 100
RH	47%	83	**36**	10 %	X 10
SAI	9mm	210	**201**	50 mm	X 50
WCR	1%	86%	**85%**	10%	X 10
WD	784mm	2735	**1951**	100 mm	X 100
MI	0.041	0.524	**0.48**	0.1 *	divided by 10

In the regression models a change of 0.9‰ per 1°C is seen. Thus the prediction is that with an increase in MAT of 1°C this will lead to an increase of 0.9‰ (B = 0.876) in $\delta^{13}C_{enamel}$. The influence of the SAI was less marked, with a 50 point change in SAI resulting in an increase of 0.6‰ (B = 0.012 x 50) in $\delta^{13}C_{enamel}$. For both MAT and SAI, the adjusted r^2 values were 0.75, indicating that the model explained a large portion of the change in $\delta^{13}C_{enamel}$.

For carnivores (Table 5.7), correlations with all meteorological factors were significant (p <0.05), although the r^2 values were lower than for ungulates.

Table 5. 7 Summary outcome of regression models for $\delta^{13}C_{enamel}$ of carnivores against each meteorological factor individually. The adjusted r^2 is modified for the number of predictors in the model. For models with only one predictor, r^2 should suffice, but for consistency r^2 adjusted is reported. B is the unstandardised regression coefficient (the change in the isotope value with a one unit change in meteorological factor); t is the test statistic (used to test whether B is significantly different from zero). *p*-values that are significant at <0.05 are in bold. Mean annual precipitation (MAP), mean annual temperature (MAT), mean annual soil moisture stress (MASMS), mean annual potential evapotranspiration (MAPE), relative humidity (RH), summer aridity index (SAI), winter concentration of rainfall (WCR), moisture index (MI) and water deficit (WD).

					95% confidence interval			
Met. factors	B	Std. error	t	*p*	Lower bound	Upper bound	r^2	r^2 adj
MAP	-0.008	0.002	-4.635	**<0.001**	-0.011	-0.004	0.41	0.39
MAT	1.969	0.328	6.004	**<0.001**	1.300	2.637	0.54	0.52
MASMS	0.338	0.047	7.161	**<0.001**	0.241	0.435	0.68	0.67
MAPE	0.004	0.001	5.164	**<0.001**	0.003	0.006	0.46	0.45
RH	-0.171	0.032	-5.368	**<0.001**	-0.236	-0.106	0.48	0.47
SAI	0.012	0.005	2.189	**0.036**	0.001	0.023	0.13	0.11
WCR	-0.062	0.015	-4.232	**<0.001**	-0.092	-0.032	0.37	0.35
WD	0.003	0.001	5.207	**<0.001**	0.002	0.004	0.47	0.45
MI	-10.994	2.588	-4.248	**<0.001**	-16.273	-5.716	0.37	0.35

The same type of analysis performed on primates showed poor relationships with most meteorological factors (Table 5.8). The r^2 values were low, indicating that the model does not adequately describe the relationship between $\delta^{13}C_{enamel}$ and the meteorological factors.

Table 5. 8 Summary outcome of regression models for $\delta^{13}C_{enamel}$ of primates against each meteorological factor individually. The adjusted r^2 is modified for the number of predictors in the model. For models with only one predictor, r^2 should suffice, but for consistency r^2 adjusted is reported. B is the unstandardised regression coefficient (the change in the isotope value with a one unit change in meteorological factor); t is the test statistic (used to test whether B is significantly different from zero). *p*-values that are significant at <0.05 are in bold. Mean annual precipitation (MAP), mean annual temperature (MAT), mean annual soil moisture stress (MASMS), mean annual potential evapotranspiration (MAPE), relative humidity (RH), summer aridity index (SAI), winter concentration of rainfall (WCR), moisture index (MI) and water deficit (WD).

					95% confidence interval			
Met factors	B	Std. error	t	*p*	Lower bound	Upper bound	r^2	r^2 adj
MAP	-0.004	0.001	-3.722	**<0.001**	-0.006	-0.002	0.09	0.08
MAT	0.778	0.254	3.062	**0.003**	0.276	1.280	0.06	0.06
MASMS	0.270	0.050	5.429	**<0.001**	0.172	0.369	0.18	0.18
MAPE	0.003	0.001	3.794	**<0.001**	0.001	0.004	0.09	0.09
RH	-0.007	0.025	-0.298	0.766	-0.057	0.042	0.00	0.01
SAI	0.002	0.002	0.798	0.426	-0.003	0.007	0.00	0.00
WCR	-0.044	0.009	-5.074	**<0.001**	-0.061	-0.027	0.15	0.15
WD	0.002	0.000	3.857	**<0.001**	0.001	0.003	0.09	0.09
MI	-6.291	1.556	-4.044	**<0.001**	-9.366	-3.216	0.10	0.10

5.3.3.3 Multiple regression

There are various approaches for attempting to identify a 'best model' in the presence of multicollinearity. The approach used here (running a series of models) was detailed in Section 4.5. Models that had multicollinearity problems were discarded. The selection process led to SAI and RH being included in the $\delta^{13}C_{enamel}$ model. For ungulates (Table 5.9), the adjusted r^2 was high (0.75), but since it was similar to the values from previous models which used one meteorological factor at a time, there seems to be no substantial advantage in using a more complicated model that includes two or more meteorological factors.

Table 5. 9 The output of the ungulate 'best fit' regression model using relative humidity (RH) and summer aridity index (SAI). r^2= 0.760 (Adjusted r^2 = 0.753).

					95% confidence interval	
Parameter	B	Std. error	t	*p*	Lower bound	Upper bound
Intercept	-16.696	1.573	-10.614	0.000	-19.792	-13.600
[FeederType=Browser]	0.407	0.959	0.425	0.671	-1.480	2.295
[FeederType=Grazer]	9.480	0.963	9.843	0.000	7.584	11.376
[FeederType=Mixed]	5.787	0.983	5.888	0.000	3.853	7.722
[FeederType=Omnivore]	0*					
[Size=Extra-large]	1.519	1.303	1.166	0.245	-1.046	4.084
[Size=Large]	0.292	0.589	0.495	0.621	-0.868	1.451
[Size=Medium]	-2.599	0.796	-3.263	0.001	-4.167	-1.031
[Size=Small]	0					
RH	0.027	0.016	1.740	0.083	-0.004	0.059
SAI	0.013	0.003	4.993	0.000	0.008	0.019

For carnivores, the r^2 from the combination best fit model (r^2 = 0.45) was no higher than some of the meteorological factors on their own (e.g., MAT, MASMS and RH) (Table 5.10). Moreover, since SAI was not significant, the model implied that using RH was sufficient. For primates, the combination of SAI and RH in the best fit model was not significant (Table 5.11).

Table 5. 10 The output of the carnivore 'best fit' regression model using relative humidity (RH) and summer aridity index (SAI). r^2= 0.483 (Adjusted r^2 = 0.449).

Parameter	B	Std. error	t	*p*	95% confidence interval	
					Lower bound	Upper bound
Intercept	-1.129	2.820	-0.400	0.692	-6.889	4.630
SAI	0.002	0.005	0.316	0.754	-0.008	0.012
RH	-0.166	0.037	-4.506	0.000	-0.241	-0.090

Table 5. 11 The output of the primate 'best fit' regression model using relative humidity (RH) and summer aridity index (SAI). r^2 = 0.006 (Adjusted r^2 = -0.008)

Parameter	B	Std. error	t	*p*	95% confidence interval	
					Lower bound	Upper bound
Intercept	-13.263	1.830	-7.248	.000	-16.881	-9.646
SAI	.002	.002	.879	.381	-.003	.007
RH	-.012	.026	-.479	.633	-.063	.038

5.3.3.4 Regression models by species-specific subsets

To remove possible variation caused by multiple species being grouped together, $\delta^{13}C_{enamel}$ values for a single species were regressed against environmental variables. This could be done only for a grazer, the red hartebeest (samples collected from five biomes) and a browser, the eland (four biomes).

Table 5.12 shows that for both species, correlations with MAT were significant. For red hartebeest, correlations with SAI and WCR are also significant, while for eland, it was MAPE, RH and WD. However, it is important to point out that the numbers of data points in the single-species analyses were markedly reduced, which may in part explain this pattern.

Table 5. 12 The r^2 (r^2 adj) values of the relationship between the $\delta^{13}C_{enamel}$ value and each of the meteorological factors, for the two species (red hartebeest and eland) for which data is available at multiple sites. **. Correlation is significant at the 0.01 level (2-tailed). *. Correlation is significant at the 0.05 level (2-tailed).

Met. values	Red hartebeest (grazer)	Eland (browser)
MAP	0.02 (-0.02)	0.09 (0.06)
MAT	0.24 (0.21)**	0.19 (0.16)*
MASMS	0.01 (-0.02)	0.10 (0.07)
MAPE	0.00 (-0.03)	0.14 (0.11)*
RH	0.03 (-0.01)	0.13 (0.11)*
SAI	0.37 (0.34)**	0.01 (0.03)
WCR	0.21 (0.18)*	0.12 (0.09)
WD	0.01 -(0.03)	0.13 (0.10)*
MI	0.01 (0.03)	0.11 (0.08)

5.3.4 $\delta^{13}C_{enamel}$ Summary

The $\delta^{13}C_{enamel}$ values reported above were grouped by biome and by animal type. Browsers (as C_3 feeders) were expected to be similar from biome to biome, but there were clear differences between the various environmental contexts. These differences were probably due partly to variations in the $\delta^{13}C$ values of C_3 plants and partly to the inclusion of small amounts of C_4 grasses and/or CAM plants, especially in areas that receive mild to moderate summer rainfall, although the distinction between the two influences cannot be made. One implication of this is that browsers appear to be more sensitive environmental proxies than previously recognised. In the Fynbos, Forest and Nama Karoo biomes, sample numbers for grazers were limited, reflecting the scarcity of grazing species in environments where there is relatively little grass. Some grazers yielded less negative $\delta^{13}C_{enamel}$ values, even in the Fynbos biome, and this is likely due to dietary selection for palatable C_4 grasses. The only mixed feeder species studied (springbok) had $\delta^{13}C_{enamel}$ values that were similar to browsers rather than grazers, suggesting that these animals were mainly browsing.

The meteorological factors that best predict the isotope values for ungulates are MAT, SAI and WCR, whereas the $\delta^{13}C_{enamel}$ for carnivores can be predicted using many of the meteorological factors (with MASMS showing the highest correlation and SAI showing the lowest). The regression model indicated that primate $\delta^{13}C_{enamel}$ was poorly correlated with meteorological factors, which may be because baboons can more easily change behaviour to suit their environment than other animals.

5.4 $\delta^{18}O_{enamel}$

5.4.1 General observations

$\delta^{18}O_{enamel}$ values in this study ranged between -11.3‰ and +10.7‰. Appendix 7 lists $\delta^{18}O_{enamel}$ values for individual animals, along with the $\delta^{13}C_{enamel}$ values. Where more than one tooth was sampled, averages are reported for that individual. As the data are not normally distributed (Appendix 6 gives details of tests to ascertain this), I evaluated the data using non-parametric approaches, giving medians (though means and standard deviations are listed in Appendix 8b). $\delta^{18}O_{enamel}$ values for ungulates (the largest group) ranged from -11.3‰ to 10.7‰ (median = 1.8‰, n = 297), while those for carnivores ranged between -10.0‰ and 2.2‰, with a median of -2.5‰, n = 33. $\delta^{18}O_{enamel}$ for primates ranged between -9.3‰ and 2.7‰, with a median value of -0.7‰, n = 146. Table 5.13 summarises the descriptive statistics for each grouping for all biomes combined. Carnivores were significantly different from primates (p = 0.040) and ungulates (p < 0.001), and primates were significantly different from ungulates (p < 0.001).

Table 5. 13 Descriptive statistics for $\delta^{18}O_{enamel}$ (‰) by faunal category.

Animal type	Feeder type	N	$\delta^{18}O$ (‰) (median)	Minimum	Maximum
Carnivore	Carnivore	33	-2.5	-10	2.2
Primate	Omnivore	146	-0.7	-9.3	2.7
Ungulate		297	1.8	-11.3	10.7
Browser	Browser	121	1.8	-9.2	9.9
Grazer	Grazer	121	1.1	-10.8	10.7
Mixed	Mixed feeder	41	4.8	-0.5	10.1
Omnivore	Omnivore	14	-5.3	-11.3	-3.1

Figure 5.9 illustrates the results in a box plot, this time by feeder type, showing significant differences between groups (Kruskal-Wallis H (4) = 147, p < 0.000). The values for carnivores and omnivores were lower than those of browsers, grazers and mixed feeders. The ranges of values were similar (p = 0.433) for browsers and grazers (-10‰ to +10‰). The mixed feeders were significantly different from all other groups (p < 0.001). The omnivore values were more negative than those of other groups, perhaps because omnivores obtain more of their water from drinking water rather than from food, compared with ungulates.

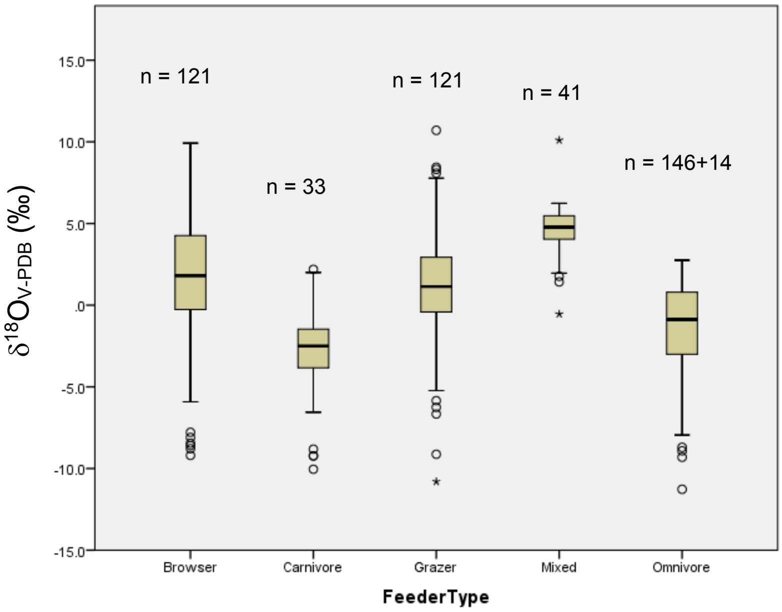

Figure 5. 9 $\delta^{18}O_{enamel}$ (‰) by feeding preference for all biomes. Omnivores include primates (n=146) and omnivorous ungulates (n=14). Bold horizontal lines indicate the median, with surrounding boxes representing the interquartile range (first quartile to third quartile). The whiskers indicate the range of values that are not outliers. Outliers (values between 1.5 and 3 times the interquartile range away from the median) are indicated by open circles and extreme outliers (values more than 3 times the interquartile range away from the median) are indicated by stars.

5.4.2 By feeding preference

5.4.2.1 Ungulates

To investigate differentiation between $\delta^{18}O_{enamel}$ values by biome, ungulates were divided into groups based on diet preference. For browsers (Figure 5.10a), $\delta^{18}O_{enamel}$ varied significantly by biome (Kruskal-Wallis H (5) = 60.76, p < 0.001). The most positive values occurred in the Savanna biome (median = 6.2‰, n = 21) while the most negative values occurred in the Forest biome (median = -5.9‰, n = 11). Values for the Forest biome were significantly different (p<0.001) from all other biomes except Albany Thicket (p=0.066): Fynbos and Succulent Karoo biomes displayed similar medians (p=0.150) of 1.0‰ and 2.5‰ respectively. There were significant differences between the Savanna biome and the Albany Thicket (p < 0.001), Fynbos (p = 0.001) and Succulent Karoo (p = 0.002). The range for the Succulent Karoo was slightly larger than for the other biomes, possibly due to more samples in this region. The map in Figure 5.11a illustrates the $\delta^{18}O_{enamel}$ values per collection location. The Fynbos biome has a wide range of values by location.

For the grazing species, $\delta^{18}O_{enamel}$ also varied significantly by biome (Kruskal-Wallis H (4) = 63.44, p < 0.001). The Fynbos biome exhibited the most consistently low $\delta^{18}O_{enamel}$ values (Figure 5.10b) although the sample size was small. Values for the Fynbos biome overlapped with those for Albany Thicket. $\delta^{18}O$ values for grasses are less affected by evaporative enrichment (Helliker and Ehleringer 2002). As grasses are less sensitive to changes in evaporation, the $\delta^{18}O_{enamel}$ values for the grazing species also show less variation across biomes. Figure 5.11b illustrates that values for the Savanna biome were most positive and significantly different from the Albany Thicket and Fynbos biomes ($p < 0.001$). There was also a significant difference between the Albany Thicket and the Succulent Karoo ($p < 0.000$).

For springbok (the only mixed feeding species) (Figure 5.10c), a Kruskal-Wallis test revealed that the $\delta^{18}O_{enamel}$ distributions of animals from different biomes displayed no statistically significant differences (H (2) = 1.02, $p = 0.601$). Location data (Figure 5.11c) shows that individual locations within the Succulent Karoo biome were more negative than individual locations within the Nama Karoo biome. The values become more positive going from west to east.

Omnivorous ungulates (bushpigs) were collected mostly from the Forest biome, with one animal from the Fynbos biome. This individual from the Fynbos biome was more enriched than those from the Forest biome (Figures 5.10d and 5.11d).

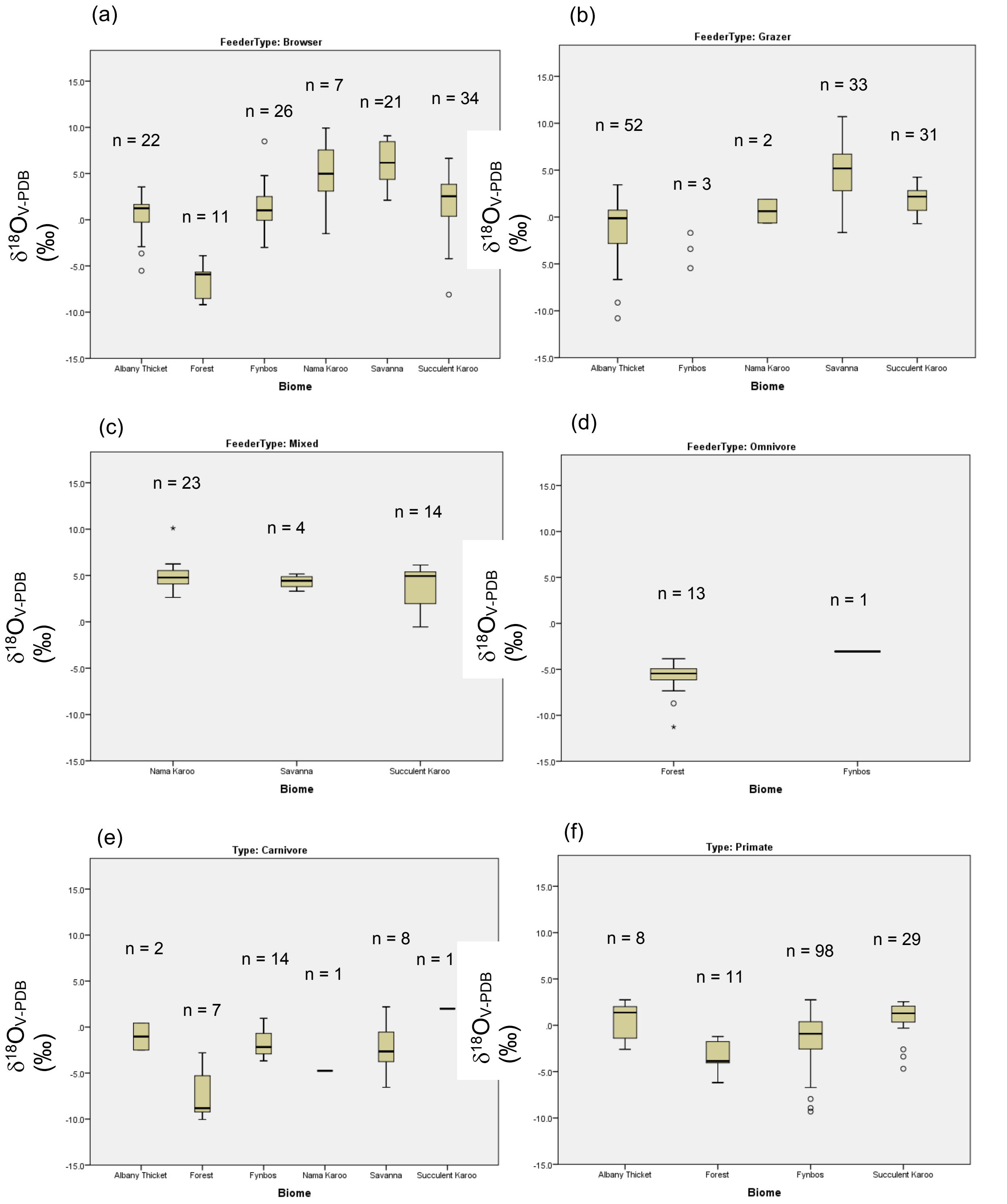

Figure 5. 10 $\delta^{18}O_{enamel}$ (‰) of a) browsers, b) grazers, c) mixed feeders, d) omnivorous ungulates, e) carnivores and f) primates. See legend to Fig. 5.9 for an explanation of the format of the plots.

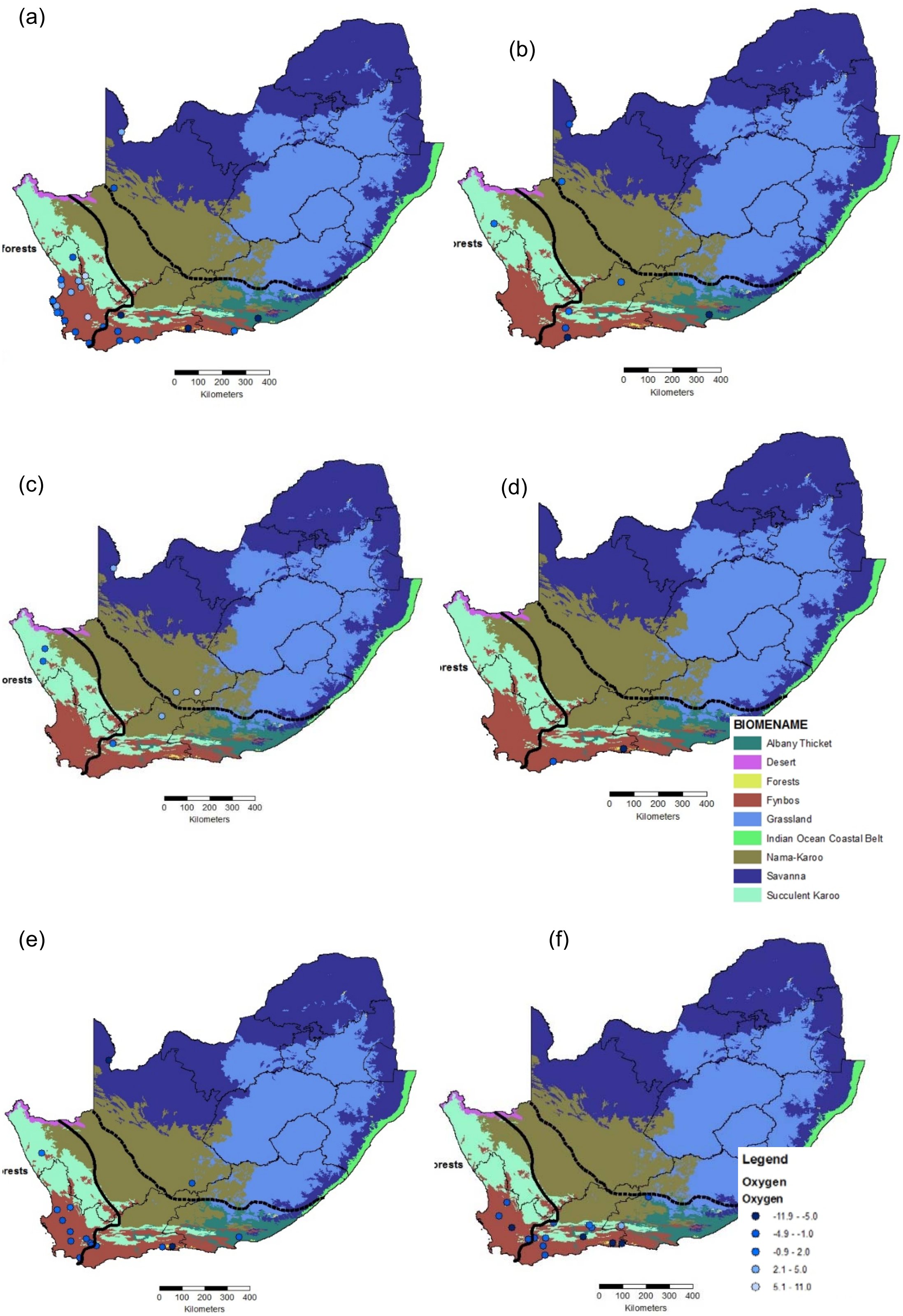

Figure 5. 11 $\delta^{18}O_{enamel}$ (‰) of a) browsers, b) grazers, c) mixed feeders, d) omnivorous ungulates, e) carnivores and f) primates by collection location across the sampled biomes. Circles represent means per collection location. The solid line indicates the approximate extent of the winter rainfall zone, the dotted line indicates the beginning of the summer rainfall zone and the area between the lines indicates the year-round rainfall zone.

5.4.2.2 Carnivores

Figure 5.10e summarises the carnivore $\delta^{18}O_{enamel}$ data by biome. There were significant differences between biomes (Kruskal-Wallis H (5) = 16.03, *p* < 0.001), but sample sizes may be too small to confirm a pattern. The lowest values were seen in the Forest biome (median = -8.8‰, n = 7) which were significantly different from the Fynbos biome (*p* = 0.012). Savanna and Forest biomes were not significantly different (*p* = 0.158). The numbers of samples from the other biomes were too small for meaningful comparisons. Fynbos and Savanna biomes were not significantly different (*p* = 0.608). As illustrated in Figure 5.11e, carnivores from all locations were depleted in ^{18}O (Figure 5.11e).

5.4.2.3 Primates

The primate species sampled consisted mainly of chacma baboons with two vervet monkey specimens. The primate $\delta^{18}O_{enamel}$ values, along with the carnivores, were consistently lower than the ungulate groups. Values from the Forest biome (Figure 5.10f) were the lowest (median = -3.9‰, n = 11), while the medians from the Succulent Karoo and Albany Thicket were the most positive, at 1.3‰ (n = 29) and 1.4‰ (n = 8) respectively. The median for the Fynbos biome was -0.9‰ (n = 98). The Forest biome differed significantly from Succulent Karoo (*p* < 0.001) and Albany Thicket (*p* = 0.002)). There was also a difference between the Fynbos biome and Succulent Karoo (*p* < 0.001). However, there was a large range of values in the Fynbos biome, which is most likely associated with the greater climatic variation within this biome. Figure 5.11f represents the individual locations with mean $\delta^{18}O_{enamel}$ values per location.

5.4.3 By biome

In the Forest biome, $\delta^{18}O_{enamel}$ values for carnivores were the most negative (median=-8.8‰, n = 7) and the values for omnivores were the highest (median=-4.9‰, n = 24) (Figure 5.12a). Although comparisons of all three groups showed that they were significantly different (Kruskal-Wallis H (2) = 8.362, *p* = 0.015), no significant differences were found through posthoc pairwise testing (carnivore: omnivore *p* = 0.123, carnivore: browser *p* = 1.000 and browser: omnivore *p* =0.134). Since no samples of tooth enamel were obtained from grazers in this biome, no comparisons between browsers and grazers could be made.

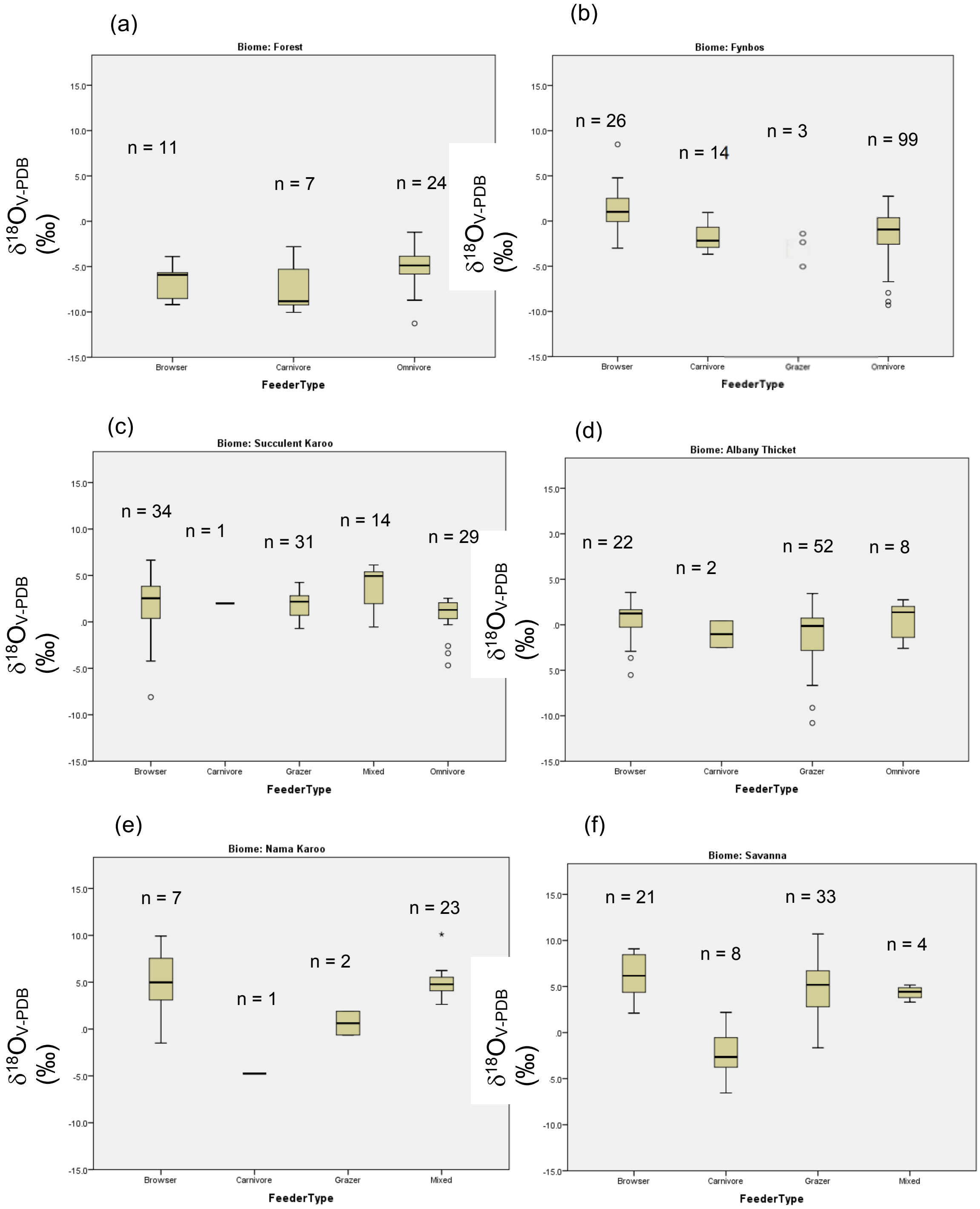

Figure 5. 12 $\delta^{18}O_{enamel}$ (‰)for the a) Forest, b) Fynbos, c), Succulent Karoo, d) Albany Thicket, e) Nama Karoo and f) Savanna biomes by feeder type. See legend to Fig. 5.9 for an explanation of the format of the plots.

In the Fynbos biome, there were significant pair-wise differences between browsers and all three of the other groups: grazers (p < 0.020), carnivores (p < 0.001) and omnivores (p < 0.001) (Kruskal-Wallis H (4) = 56.31, p < 0.001) (Figure 5.12b). The sample size and range for omnivores was much larger than for any other group. Although there were only three grazing individuals in this biome, it is worth noting they were more depleted in ^{18}O than the browsers (p = 0.020).

In the Succulent Karoo biome, mixed feeders were most positive, with a median $\delta^{18}O_{enamel}$ of 4.9‰ (n = 14), while omnivores were lowest, with a median $\delta^{18}O_{enamel}$ of 1.3‰ (n = 29) (Figure 5.12c). Mixed feeders were significantly different from omnivores (*p* < 0.001) and grazers (*p* = 0.040). Browsers and grazers were not significantly different from each other (*p* = 1.000).

In the Albany Thicket biome, there were no significant differences in $\delta^{18}O_{enamel}$ between any of the feeder types (Kruskal-Wallis test H (3) = 8.76, *p* = 0.058) (Figure 5.12d).

Sample numbers from the Nama Karoo were low, which means it is not possible to reliably determine if there are differences (Figure 5.12e). Thus a Kruskal-Wallis indicates there are no significant differences (H (3) = 7.34, *p* = 0.062). Sample numbers were largest for browsers (n = 7) and mixed feeders (n = 23). No conclusions can be drawn about patterning in $\delta^{18}O_{enamel}$ in this biome.

In the Savanna biome, there were significant differences in the four groups of animals (Kruskal-Wallis H (3) = 21.54, *p* < 0.000) (Figure 5.12f). Browsing species were the most positive (median= 6.2‰, n = 21). Carnivores were the most negative (median= -2.7‰, n = 8). Carnivores were significantly different from grazers (*p* = 0.001) and browsers (*p* < 0.001) but not from mixed feeders (*p* = 0.166). A larger sample size may have revealed a significant difference. Browsers were not significantly different from grazers (*p* = 0.764).

5.4.4 By isotopic sensitivity to environmental aridity

5.4.4.1 Across biomes

$\delta^{18}O_{enamel}$ values of evaporation sensitive (ES[22]) (Figure 5.13a) and water independent (WI[23]) (Figure 5.13b) ungulates were compared across different biomes. Among ES animals, there were significant differences between biomes (Kruskal-Wallis H (5) = 86.95, *p* < 0.001). The Forest biome showed the lowest values, with a median of -6.8‰ (n = 10). The Nama Karoo had the most positive values (median = 4.9‰; n = 30). The Forest biome was significantly different from the Savanna, Succulent Karoo and Nama Karoo biomes (*p* < 0.001) (Table 5.14). The Nama Karoo biome was significantly different to the Fynbos biome (*p* < 0.001), Succulent Karoo (*p* = 0.005) and Albany Thicket (*p* < 0.001) (Table 5.13 lists all *p*-values). The Savanna biome was significantly different from the Succulent Karoo and Albany Thicket biomes (*p* < 0.001). The Albany Thicket biome was also significantly different to the Succulent Karoo (*p* = 0.044).

[22] ES animals include the blue duiker, bushbuck, common duiker, eland, giraffe, grey rhebuck, grysbok, klipspringer, kudu, springbok, steenbok, and southern reedbuck.
[23] WI animals include blue duiker, common duiker, eland, gemsbok, grey rhebuck, grysbok, klipspringer, red hartebeest, springbok, steenbok, and warthog.

A similar result was found among WI animals (Kruskal-Wallis H (5) = 86.95, p < 0.000) with significant differences found in the same pairs of biomes (Figure 5.13b, Table 5.14 for p-values). The Forest biome had the most negative $\delta^{18}O_{enamel}$ values (median = -5.9‰, n = 6). Nama Karoo and Savanna biomes had the most positive $\delta^{18}O_{enamel}$ values (median =4.9‰, n = 29 and median = 5.3‰, n = 45, respectively). Refer to Appendix 8b for $\delta^{18}O_{enamel}$ values.

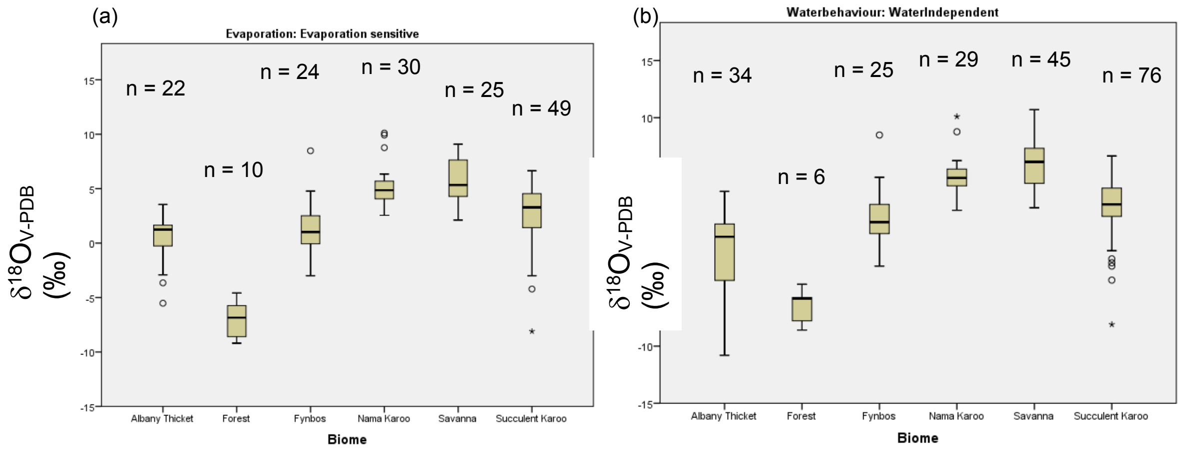

Figure 5. 13 $\delta^{18}O_{enamel}$ (‰) of a) evaporation sensitive ungulates and b) water independent ungulates by biome. See legend to Fig. 5.9 for an explanation of the format of the plots.

Table 5. 14 The *p*-values for each of the pairwise comparisons for a) evaporation sensitive and b) water independent ungulates.

(a)

Sample1-Sample2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj.Sig.
Forest-Albany Thicket	37.391	17.670	2.116	.034	.515
Forest-Fynbos	-50.862	17.439	-2.917	.004	.053
Forest-Succulent Karoo	-72.769	16.077	-4.526	.000	.000
Forest-Nama Karoo	-111.600	16.918	-6.596	.000	.000
Forest-Savanna	-117.240	17.336	-6.763	.000	.000
Albany Thicket-Fynbos	-13.472	13.676	-.985	.325	1.000
Albany Thicket-Succulent Karoo	-35.378	11.891	-2.975	.003	.044
Albany Thicket-Nama Karoo	-74.209	13.005	-5.706	.000	.000
Albany Thicket-Savanna	-79.849	13.544	-5.895	.000	.000
Fynbos-Succulent Karoo	-21.907	11.544	-1.898	.058	.866
Fynbos-Nama Karoo	-60.738	12.689	-4.787	.000	.000
Fynbos-Savanna	-66.378	13.241	-5.013	.000	.000
Succulent Karoo-Nama Karoo	38.831	10.741	3.615	.000	.005
Succulent Karoo-Savanna	44.471	11.388	3.905	.000	.001
Nama Karoo-Savanna	-5.640	12.547	-.450	.653	1.000

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.
Asymptotic significances (2-sided tests) are displayed. The significance level is .05.

(b)

Sample1-Sample2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj.Sig.
Forest-Albany Thicket	33.304	27.547	1.209	.227	1.000
Forest-Fynbos	-69.073	28.281	-2.442	.015	.219
Forest-Succulent Karoo	-92.570	26.380	-3.509	.000	.007
Forest-Nama Karoo	-147.454	27.901	-5.285	.000	.000
Forest-Savanna	-162.078	27.037	-5.995	.000	.000
Albany Thicket-Fynbos	-35.769	16.390	-2.182	.029	.436
Albany Thicket-Succulent Karoo	-59.266	12.835	-4.617	.000	.000
Albany Thicket-Nama Karoo	-114.150	15.725	-7.259	.000	.000
Albany Thicket-Savanna	-128.774	14.136	-9.110	.000	.000
Fynbos-Succulent Karoo	-23.497	14.343	-1.638	.101	1.000
Fynbos-Nama Karoo	-78.381	16.978	-4.617	.000	.000
Fynbos-Savanna	-93.004	15.518	-5.993	.000	.000
Succulent Karoo-Nama Karoo	54.884	13.578	4.042	.000	.001
Succulent Karoo-Savanna	69.508	11.701	5.940	.000	.000
Nama Karoo-Savanna	-14.624	14.814	-.987	.324	1.000

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.
Asymptotic significances (2-sided tests) are displayed. The significance level is .05.

For the evaporation insensitive (EI[24]) animals (Figure 5.14a) significant differences were also found (Kruskal-Wallis H (5) = 85.386, $p < 0.000$). Pairwise comparisons with adjusted *p*-values showed that there were significant differences between the Forest biome and each of the following biomes: Savanna ($p < 0.001$); Succulent Karoo ($p < 0.001$); and Albany Thicket ($p = 0.028$). The Fynbos biome differed significantly from the Savanna biome ($p = 0.001$). There was also a significant difference between the Albany Thicket biome and the Succulent Karoo ($p = 0.001$) and Savanna ($p < 0.001$). When looking at the water dependent (WD[25]) animals (Figure 5.14b), it was only the Forest biome that was significantly different from all other biomes except the Fynbos biome (Kruskal-Wallis H (5) = 45.931, $p < 0.001$) (Table 5.15 for *p*-values).

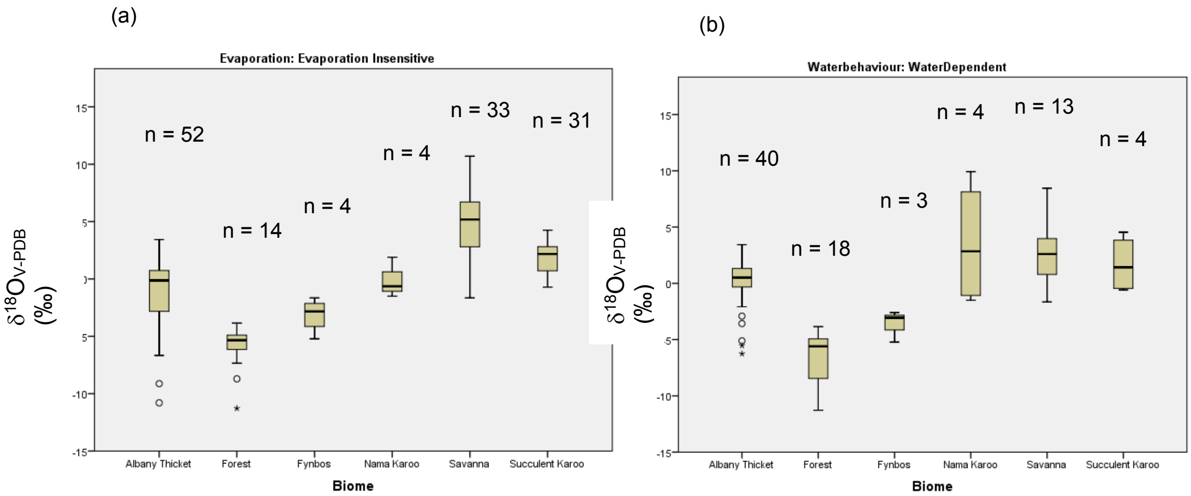

Figure 5. 14 $\delta^{18}O_{enamel}$ (‰) of a) evaporation insensitive and b) water dependent ungulate species by biome. Bold horizontal lines indicate the median, with surrounding boxes representing the interquartile range (first quartile to third quartile). The whiskers indicate the range of values that are not outliers. Outliers (values of between 1.5 and 3 more than the interquartile range) are indicated by an open circle and extreme outliers (values more than 3 times the interquartile range away from the median) are indicated by a solid star.

[24] EI animals include the black rhino, blue wildebeest, bontebok, buffalo, bushpig, gemsbok, hippopotamus, red hartebeest, warthog, and mountain zebra.
[25] WD animals include black rhino, blue wildebeest, bontebok, buffalo, bushbuck, bushpig, giraffe, hippopotamus, kudu, mountain zebra, and southern reedbuck.

Table 5. 15 The p-values for each of the pairwise comparisons of biomes for a) evaporation insensitive and b) water dependent ungulates.

(a)

Sample1-Sample2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj.Sig.
Forest-Fynbos	-12.625	22.504	-.561	.575	1.000
Forest-Albany Thicket	37.212	11.951	3.114	.002	.028
Forest-Nama Karoo	-41.250	25.253	-1.633	.102	1.000
Forest-Succulent Karoo	-72.960	12.781	-5.708	.000	.000
Forest-Savanna	-96.917	12.660	-7.655	.000	.000
Fynbos-Albany Thicket	24.587	20.595	1.194	.233	1.000
Fynbos-Nama Karoo	-28.625	30.316	-.944	.345	1.000
Fynbos-Succulent Karoo	-60.335	21.088	-2.861	.004	.063
Fynbos-Savanna	-84.292	21.015	-4.011	.000	.001
Albany Thicket-Nama Karoo	-4.038	23.568	-.171	.864	1.000
Albany Thicket-Succulent Karoo	-35.748	9.007	-3.969	.000	.001
Albany Thicket-Savanna	-59.705	8.834	-6.759	.000	.000
Nama Karoo-Succulent Karoo	-31.710	24.000	-1.321	.186	1.000
Nama Karoo-Savanna	-55.667	23.935	-2.326	.020	.301
Succulent Karoo-Savanna	23.957	9.928	2.413	.016	.237

(b)

Sample1-Sample2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj.Sig.
Forest-Fynbos	-10.194	14.851	-.686	.492	1.000
Forest-Albany Thicket	35.669	6.759	5.277	.000	.000
Forest-Nama Karoo	-44.444	13.164	-3.376	.001	.011
Forest-Succulent Karoo	-44.694	13.164	-3.395	.001	.010
Forest-Savanna	-50.925	8.668	-5.875	.000	.000
Fynbos-Albany Thicket	25.475	14.256	1.787	.074	1.000
Fynbos-Nama Karoo	-34.250	18.189	-1.883	.060	.895
Fynbos-Succulent Karoo	-34.500	18.189	-1.897	.058	.868
Fynbos-Savanna	-40.731	15.254	-2.670	.008	.114
Albany Thicket-Nama Karoo	-8.775	12.489	-.703	.482	1.000
Albany Thicket-Succulent Karoo	-9.025	12.489	-.723	.470	1.000
Albany Thicket-Savanna	-15.256	7.603	-2.007	.045	.672
Nama Karoo-Succulent Karoo	-.250	16.840	-.015	.988	1.000
Nama Karoo-Savanna	-6.481	13.617	-.476	.634	1.000
Succulent Karoo-Savanna	6.231	13.617	.458	.647	1.000

5.4.4.2 By biome

Comparing the categories EI/ES and WI/WD within each biome was another useful way to examine the data. In most biomes, ES animals were more enriched in ^{18}O than EI ones (Figure 5.15): Nama Karoo (Mann-Whitney Z value 2.641, p < 0.001), Albany Thicket (Z = 2.060, p = 0.009), Fynbos (Z = 2.465, p = 0.002), Succulent Karoo (Z = 3.284, p = 0.039). The Savanna and Forest biomes showed no significant differences between EI and ES animals (Savanna: Mann-Whitney Z value 2.152, p = -0.44; Forest: Mann-Whitney Z = -3.216, p = 0.001).

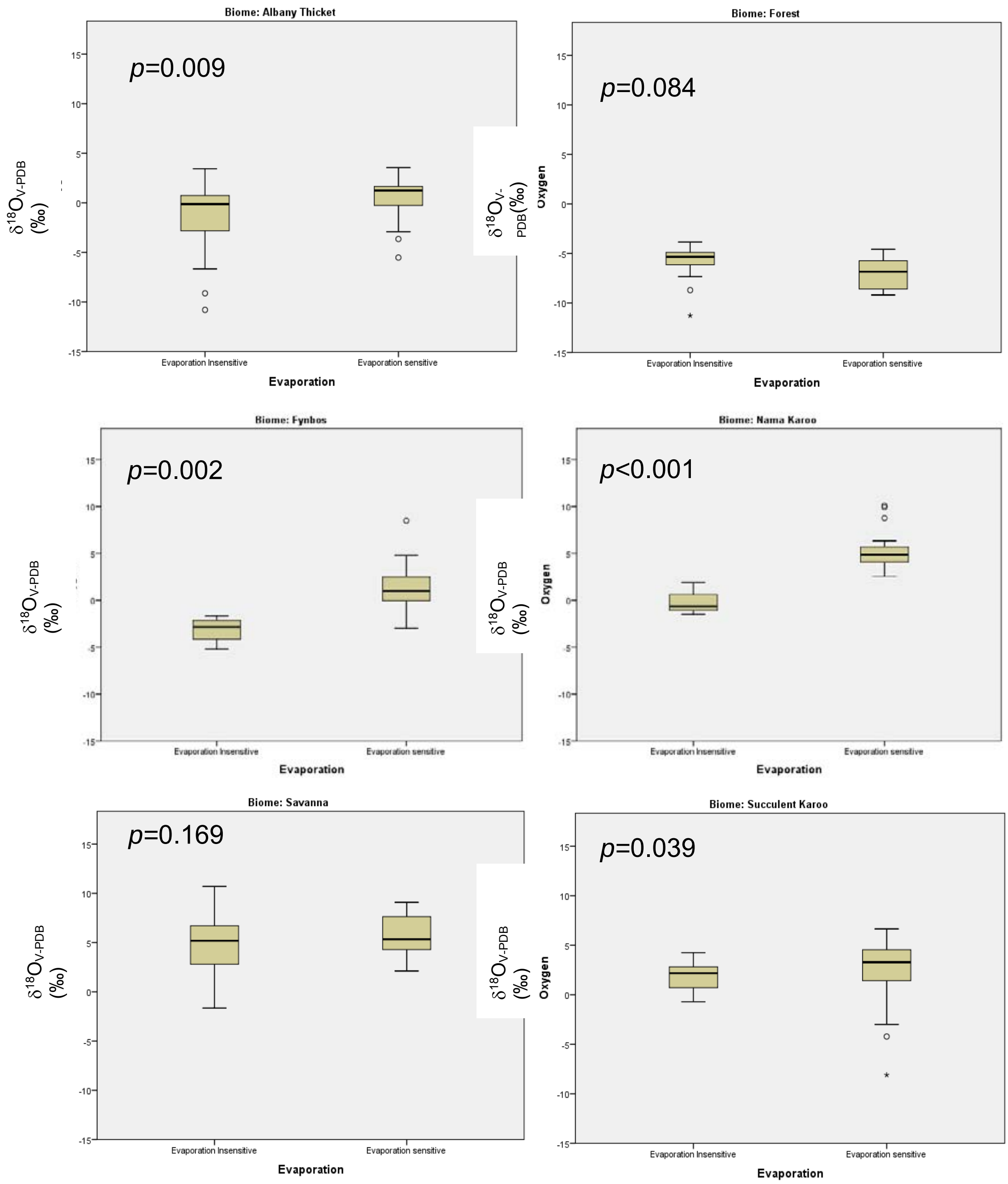

Figure 5. 15 Comparison of $\delta^{18}O_{enamel}$ for ES and EI ungulates per biome. See legend to Fig. 5.5 for an explanation of the format of the plots.

Patterns were slightly different when species were grouped by WD/WI (Figure 5.16). For three biomes, there was a significant difference: Albany Thicket (Z = -2.712, p = 0.014); Fynbos (Z = 2.373, p = 0.001); and Savanna (Z = 2.152, p = 0.001). The other three biomes had no significant difference. More biomes had significant differences when the data is split by ES/EI instead of WD/WI. Thus splitting the ungulate group by WD/WI reveals partitioning in the groups that the ES/EI split did not.

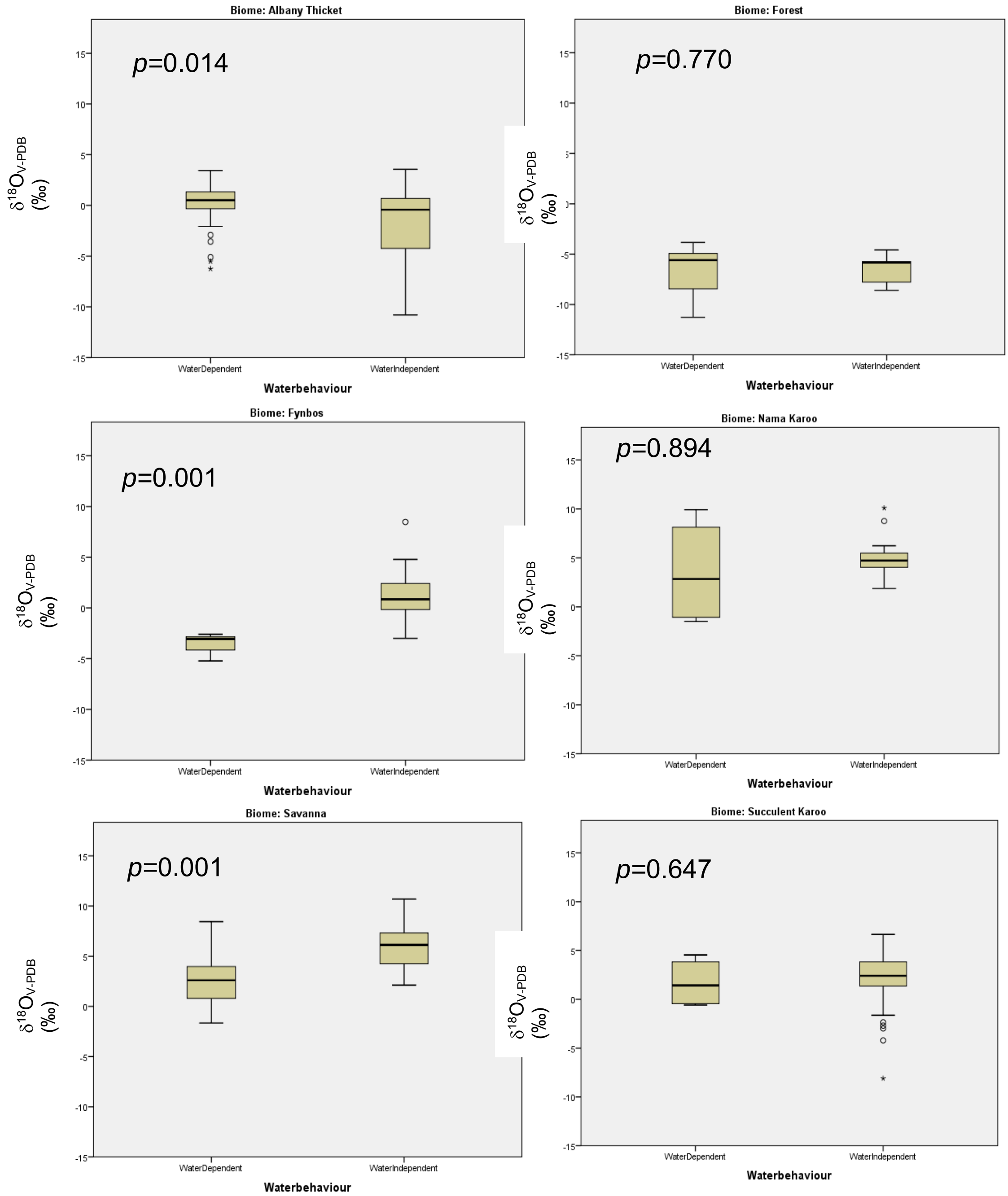

Figure 5. 16 Comparison of $\delta^{18}O_{enamel}$ for WD and WI ungulates per biome.

5.4.5 Relationships between $\delta^{18}O_{enamel}$ and meteorological factors

The relationships between $\delta^{18}O_{enamel}$ and meteorological factors were investigated in the following sections. First correlations are run and then regression models were constructed, which were used to predict the $\delta^{18}O_{enamel}$ based on a set of meteorological factors.

5.4.5.1 Correlations

Table 5.16 provides the correlation coefficients and significance of the relationships between the meteorological factors and $\delta^{18}O_{enamel}$ values per animal grouping. Correlations were considered meaningful if the significance was <0.05.

Grazer $\delta^{18}O_{enamel}$ was most significantly correlated with MASMS, WD and MAPE, while browser $\delta^{18}O_{enamel}$ was highly correlated with MAP, MAPE, WD and MI. Mixed feeders showed the fewest significant correlations, with only SAI and WCR being significant. In omnivores, $\delta^{18}O_{enamel}$ was significantly correlated with eight out of nine meteorological factors but the correlation coefficients were lower than in the grazing and browsing subsets. Five out of nine meteorological factors were significantly correlated with carnivore $\delta^{18}O_{enamel}$.

Table 5. 16 Correlation coefficients for $\delta^{18}O_{enamel}$ and meteorological variables from all locations. The number of specimens varies across the rows because not all meteorological variables are available for all locations. 'Omnivore' includes ungulate omnivores and primate omnivores. Correlation coefficients are considered significant when *p* <0.05 (in bold). Mean annual precipitation (MAP), mean annual temperature (MAT), mean annual soil moisture stress (MASMS), mean annual potential evapotranspiration (MAPE), relative humidity (RH), summer aridity index (SAI), winter concentration of rainfall (WCR), moisture index (MI) and water deficit (WD).

FeederType		MAP	MAT	MASMS	MAPE	RH	SAI	WCR	WD	MI
Browser	Correlation Coefficient (r_s)	**-0.698****	**0.300****	**0.562****	**0.729****	**-0.490****	0.021	**-0.452****	**0.724****	**-0.697****
	Sig. (2-tailed)	<.001	0.001	<0.001	<0.001	<0.001	0.820	<0.001	<0.001	<0.001
	N	121	121	110	121	121	121	121	121	121
Grazer	Correlation Coefficient (r_s)	**-0.695****	**0.338****	**0.712****	**0.715****	**-0.693****	**0.314****	**-0.326****	**0.715****	**-0.695****
	Sig. (2-tailed)	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	N	121	121	121	121	121	121	121	121	121
Mixed	Correlation Coefficient (r_s)	**0.334***	-0.264	0.000	-0.111	0.280	-0.280	-0.117	-0.241	**0.334***
	Sig. (2-tailed)	0.033	0.095	1.000	0.491	0.077	0.077	0.467	0.129	0.033
	N	41	41	41	41	41	41	41	41	41
Omnivore	Correlation Coefficient (r_s)	**-0.693****	-0.069	**0.416****	**0.610****	**-0.230****	**-0.385****	**-0.198***	**0.596****	**-0.612****
	Sig. (2-tailed)	<0.001	0.388	<0.001	<0.001	0.003	<0.001	0.012	<0.001	<0.001
	N	160	160	136	160	160	160	160	160	160
Carnivore	Correlation Coefficient (r_s)	**-0.473****	-0.116	0.043	**0.438***	0.177	**-0.507****	0.194	**0.455****	**-0.482****
	Sig. (2-tailed)	0.005	0.519	0.836	0.011	0.324	0.003	0.279	0.008	0.004
	N	33	33	26	33	33	33	33	33	33

**. Correlation is significant at the 0.01 level (2-tailed).

*. Correlation is significant at the 0.05 level (2-tailed).

Following this test, regression models were constructed, which were used to predict the $\delta^{18}O_{enamel}$ based on the meteorological factors.

5.4.5.2 Simple regression

Univariate regressions were run for $\delta^{18}O_{enamel}$ against each of the meteorological factors in order to estimate the degree of change in $\delta^{18}O_{enamel}$ values in response to unit changes in the meteorological variables. Many of the meteorological factors were strongly linearly related. Due to multicollinearity, many were not included in the regression models since regression assumes no relationship between factors in a model (refer to Appendix 3). Each factor was analysed individually to begin with, followed by combinations of factors where the relationships between them was likely to be weak ('best model').

For ungulates, fixed variables included feeder type (grazers, browsers, mixed feeders or omnivores) and size of animal (small, medium, large or extra-large). A summary of the outcome of the multiple regressions for ungulates where each of the meteorological factors was tested individually is provided in Table 5.17.

Table 5. 17 Summary outcome of regression models for $\delta^{18}O_{enamel}$ for ungulates against each meteorological factor individually. The adjusted r^2 is modified for the number of predictors in the model. For models with only one predictor, r^2 should suffice, but for consistency r^2 adjusted is reported. B is the unstandardised regression coefficient (the change in the isotope value with a one unit change in meteorological factor); t is the test statistic (used to test whether B is significantly different from zero). *p*-values that are significant at <0.05 are in bold. Mean annual precipitation (MAP), mean annual temperature (MAT), mean annual soil moisture stress (MASMS), mean annual potential evapotranspiration (MAPE), relative humidity (RH), summer aridity index (SAI), winter concentration of rainfall (WCR), moisture index (MI) and water deficit (WD).

					95% confidence interval			
Met. variables	B	Std. error	t	*p*	Lower bound	Upper bound	r^2	r^2 adj
MAP	-0.013	0.001	-12.066	**<0.001**	-0.015	-0.011	0.61	0.60
MAT	1.554	0.248	6.262	**<0.001**	1.065	2.042	0.49	0.47
MASMS	0.400	0.042	9.498	**<0.001**	0.317	0.484	0.47	0.46
MAPE	0.006	0.000	13.305	**<0.001**	0.005	0.007	0.64	0.63
RH	-0.151	0.016	-9.478	**<0.001**	-0.182	-0.120	0.56	0.54
SAI	0.001	0.003	0.173	0.862	-0.006	0.007	0.42	0.40
WCR	-0.046	0.011	-4.271	**<0.001**	-0.067	-0.025	0.45	0.44
WD	0.004	0.000	13.684	**<0.001**	0.004	0.005	0.65	0.64
MI	-20.732	1.647	-12.585	**<0.001**	-23.974	-17.489	0.62	0.61

All the meteorological factors except SAI were correlated with the $\delta^{18}O_{enamel}$ values and therefore could be used to explain some of the variation in $\delta^{18}O_{enamel}$. Using Table 5.17to fit the regression model, a change of 100 mm in mean rainfall (MAP) should result in a $\delta^{18}O$ decrease of 1.3‰ (0.013 × 100). An increase of 1◦C in MAT will result in a $\delta^{18}O_{enamel}$ increase of 1.55‰. The r^2 values indicate how much variation in $\delta^{18}O_{enamel}$ was explained by the fitted model. The r^2 values ranged between 0.35 and 0.57 for meteorological factors with *p*-values of <0.05. These values were lower than those for regressions using $\delta^{13}C_{enamel}$. Appendix 9 provides the outcome of the individual models for each meteorological factor.

For carnivores, the same regression models were run. Table 5.18 shows that MAP ($p < 0.001$), MAPE ($p = 0.019$), SAI ($p = 0.012$), WD ($p = 0.004$) and MI ($p < 0.001$) are significant.

Table 5. 18 Summary outcome of the regression models for $\delta^{18}O_{enamel}$ for carnivores against each meteorological factor individually. The adjusted r^2 is modified for the number of predictors in the model. For models with only one predictor, r^2 should suffice, but for consistency r^2 adjusted is reported. B is the unstandardised regression coefficient (the change in the isotope value with a one unit change in meteorological factor); t is the test statistic (used to test whether B is significantly different from zero). *p*-values that are significant at <0.05 are in bold. Mean annual precipitation (MAP), mean annual temperature (MAT), mean annual soil moisture stress (MASMS), mean annual potential evapotranspiration (MAPE), relative humidity (RH), summer aridity index (SAI), winter concentration of rainfall (WCR), moisture index (MI) and water deficit (WD).

Met. variables	B	Std. error	t	*p*	95% confidence interval			
					Lower	Upper	r^2	r^2 adj
MAP	-0.007	0.002	-4.220	**<0.001**	-0.011	-0.004	0.37	0.34
MAT	0.057	0.482	0.118	0.907	-0.926	1.039	0.00	-0.03
MASMS	-0.002	0.055	-0.036	0.972	-0.114	0.111	0.00	-0.04
MAPE	0.003	0.001	2.476	**0.019**	0.000	0.005	0.17	0.14
RH	-0.038	0.044	-0.866	0.393	-0.127	0.051	0.02	-0.01
SAI	-0.014	0.005	-2.655	**0.012**	-0.025	-0.003	0.19	0.16
WCR	0.017	0.018	0.959	0.345	-0.020	0.054	0.03	0.00
WD	0.002	0.001	3.108	**0.004**	0.001	0.003	0.24	0.21
MI	-11.351	2.535	-4.478	**<0.001**	-16.520	-6.181	0.39	0.37

MAP and MI had the highest r^2 values (0.34 and 0.37 respectively) so based on this sample, carnivore $\delta^{18}O_{enamel}$ was not a strong predictor of meteorological factors. Nevertheless, the results of this test suggest that with a 100 mm increase in MAP, carnivore $\delta^{18}O_{enamel}$ should decrease by 0.7‰ (0.007 × 100). Moreover, with a change of 10% in the MI, carnivore $\delta^{18}O_{enamel}$ should decrease by 1.135‰ (11.35 / 10).

For primates, correlations with all meteorological factors except MAT and WCR were significant (Table 5.19) but had low r^2 values. MAP had the highest r^2 value of 0.28. Primate $\delta^{18}O_{enamel}$ values were therefore not a good predictor of meteorological factors.

Table 5. 19 Summary outcome of the regression models for $\delta^{18}O_{enamel}$ for primates against each meteorological factor individually. The adjusted r^2 is modified for the number of predictors in the model. For models with only one predictor, r^2 should suffice, but for consistency r^2 adjusted is reported. B is the unstandardised regression coefficient (the change in the isotope value with a one unit change in meteorological factor); t is the test statistic (used to test whether B is significantly different from zero). *p*-values that are significant at <0.05 are in bold. Mean annual precipitation (MAP), mean annual temperature (MAT), mean annual soil moisture stress (MASMS), mean annual potential evapotranspiration (MAPE), relative humidity (RH), summer aridity index (SAI), winter concentration of rainfall (WCR), moisture index (MI) and water deficit (WD).

Met. variables	B	Std. error	t	*p*	95% Confidence interval		r^2	r^2 adj
					Lower	Upper		
MAP	-0.007	0.001	-7.498	**<0.001**	-0.009	-0.005	0.28	0.28
MAT	0.340	0.276	1.232	0.220	-0.206	0.887	0.01	0.00
MASMS	0.254	0.052	4.855	**<0.001**	0.151	0.358	0.15	0.14
MAPE	0.005	0.001	6.226	**<0.001**	0.003	0.006	0.21	0.21
RH	-0.108	0.025	-4.351	**<0.001**	-0.158	-0.059	0.12	0.11
SAI	-0.016	0.002	-7.267	**<0.001**	-0.020	-0.011	0.27	0.26
WCR	-0.006	0.010	-0.564	0.574	-0.025	0.014	0.00	0.01
WD	0.003	0.000	6.946	**<0.001**	0.002	0.004	0.25	0.25
MI	-10.754	1.491	-7.214	**<0.001**	-13.701	-7.808	0.27	0.26

5.4.5.3 Multiple regression

Models were fitted using each possible subset of meteorological variables that were not correlated. Models that had multicollinearity were discarded. Of the remaining models, that which provided the lowest AIC value (Refer to Data analysis section 4.5) was considered the best model. Note that different approaches for model selection or identifying multicollinearity would lead to different 'best models'. The selection process led to MAPE and WCR being included in the model. The summary for ungulates is reported below in Table 5.20.

Table 5. 20 The output of the ungulate 'best fit' model using mean annual evapotranspiration (MAPE) and winter concentration rainfall (WCR) as predictors. r^2 = 0.654 (Adjusted r^2 = 0.644).

Parameter	B	Std. error	t	*p*	95% confidence interval	
					Lower bound	Upper bound
Intercept	-16.711	1.812	-9.220	<0.001	-20.279	-13.144
[FeederType=Browser]	-0.051	0.920	-0.055	0.956	-1.863	1.761
[FeederType=Grazer]	-1.414	0.906	-1.561	0.120	-3.197	0.369
[FeederType=Mixed]	5.437	0.875	6.210	<0.001	3.714	7.160
[FeederType=Omnivore]	0*					
[Size=Extra-large]	-0.932	1.205	-0.773	0.440	-3.303	1.440
[Size=Large]	1.806	0.564	3.204	0.002	0.697	2.916
[Size=Medium]	-2.798	0.749	-3.734	<0.001	-4.273	-1.323
[Size=Small]	0*					
MAPE	0.007	0.001	12.971	<0.001	0.006	0.008
WCR	0.038	0.011	3.580	<0.001	0.017	0.059

The adjusted r^2 was 0.64, meaning that almost two thirds of the variance is explained by the model. However, referring back to Table 5.15, regression models for ungulates using one meteorological factor at a time yielded an r^2 value for MAPE of 0.63. In this case, using this single meteorological factor is as good as (or preferable to) complicated models with multiple factors.

For the regression model for carnivores (Table 5.21), the outcome was significant and the r^2 was 0.377. From Table 5.18, correlations with MI and MAP on their own had adjusted r^2 values of 0.37 and 0.34 respectively. The regression model for primates showed that the overall model had an r^2 value of 0.209, but with only MAPE as significant ($p < 0.001$) (Table 5.22).

Table 5. 21 The output of the carnivore 'best fit' model using mean annual evapotranspiration (MAPE) and winter concentration rainfall (WCR) as predictors. r^2 = 0.416 (Adjusted r^2 =0.377).

					95% confidence interval	
Parameter	B	Std. error	t	*p*	Lower bound	Upper bound
Intercept	-16.564	2.964	-5.588	0.000	-22.617	-10.511
MAPE	0.005	0.001	4.457	0.000	0.003	0.007
WCR	0.063	0.018	3.587	0.001	0.027	0.099

Table 5. 22 The output of the primate 'best fit' model using mean annual evapotranspiration (MAPE) and winter concentration rainfall (WCR) as predictors. r^2 = 0.220 (Adjusted r^2 = 0.209).

					95% confidence interval	
Parameter	B	Std. error	t	*p*	Lower bound	Upper bound
Intercept	-11.523	1.786	-6.450	0.000	-15.054	-7.992
MAPE	0.005	0.001	6.320	0.000	0.003	0.006
WCR	0.011	0.009	1.208	0.229	-0.007	0.029

5.4.5.3 Regression models by specific subsets

A regression model was run focussing on individual species in order to explore whether or not a more appropriate model could be identified at an individual level. This test attempted to remove variation caused by different species being grouped together in the sample. The species found in several biomes were used, namely red hartebeest and eland). In the case of $\delta^{18}O_{enamel}$, there was a clearer signal for eland, which is an ES animal, compared with hartebeest, which is EI (Table 5.23).

Table 5. 23 The r^2 (r^2 adj) values of the relationship between the $\delta^{18}O_{enamel}$ value and each of the meteorological factors, for the two species (red hartebeest and eland) for which data is available at multiple sites. **. Correlation is significant at the 0.01 level (2-tailed). *. Correlation is significant at the 0.05 level (2-tailed).

	Red hartebeest (grazer)	Eland (browser)
MAP	0.42 (0.4)**	0.46 (0.44)**
MAT	0.23 (0.20)**	0.53 (0.51)**
MASMS	0.47 (0.45)**	0.57 (0.55)**
MAPE	0.53 (0.51)**	0.57 (0.56)**
RH	0.49 (0.47)**	0.57 (0.55)**
SAI	0.03 (0.01)	0.46 (0.45)**
WCR	0.04 (0.01)	0.62 (0.60)**
WD	0.51 (0.49)**	0.55 (0.54)**
MI	0.44 (0.42)**	0.48 (0.47)**

Red hartebeest $\delta^{18}O_{enamel}$ is correlated significantly with all but two meteorological factors (SAI and WCR). The adjusted r^2 values range from 0.200 for MAT to 0.511 for MAPE. Eland $\delta^{18}O_{enamel}$ was significantly correlated with all meteorological factors ($p < 0.01$), with adjusted r^2 values from 0.441 for MAP to 0.604 for WCR. These tests show that using a single species of animal provides clearer relationships between $\delta^{18}O$ and environmental variables.

5.4.6 A measure of aridity for Southern Africa

Table 5.24 provides average $\delta^{18}O_{enamel}$ values for the EI (evaporation insensitive) and ES (evaporation sensitive) animals from each of the biomes, and the difference between the two.

Table 5. 24 Average $\delta^{18}O_{enamel}$ per biome for the evaporation insensitive (EI) and evaporation sensitive (ES) animal groupings and the difference (ES-EI).

Biome	EI	ES	Difference
Nama Karoo	-0.08	4.74	4.8
Fynbos	-0.93	1.57	2.5
Albany Thicket	-1.52	-0.02	1.5
Savanna	4.67	5.72	1.0
Succulent Karoo	1.87	2.39	0.5
Forest	-5.94	-7.05	-1.1

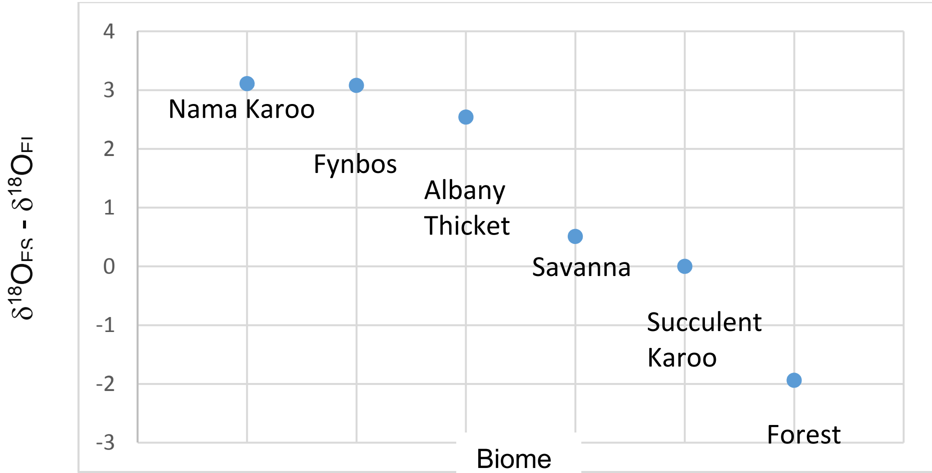

Figure 5. 17 The difference between the mean $\delta^{18}O_{enamel}$ of evaporation sensitive (ES) and insensitive (EI) animals for each biome (ES-EI).

The Nama Karoo showed the biggest difference between ES and EI animals (Figure 5.17), With the next highest value being for Fynbos. This was somewhat surprising. Albany thicket and Savanna biomes showed differences of 1.5 and 1 respectively. The succulent Karoo had a small difference of 0.5. The Forest biome had a negative difference, meaning that ES was lower than EI. These deductions are constrained by the fact that the species composition in the groups WI/WD or EI/ES are not always the same and also sample sizes differ. Thus a large sample size of a particular species that has a particularly low or high O value could influence the mean of a biome.

Table 5.25 provides the mean $\delta^{18}O_{enamel}$ values for WD and WI animals from each of the biomes. The Savanna biome showed a higher difference between WD and WI animals than all other biomes. The difference in the Fynbos biome again seemed higher than expected while the Forest biome exhibited no difference between WD and WI animals. In the Albany Thicket biome, values for WI species were more negative than those for WD (Table 5.23, Figure 5.18) because two of the three species in the WI category had very low $\delta^{18}O_{enamel}$ values (red hartebeest and warthog).

Table 5. 25 Mean $\delta^{18}O_{enamel}$ per biome for the water dependent (WD) and water independent (WI) animal groupings and the difference (WI-WD).

Biome	WD	WI	Difference
Fynbos	-1.64	1.47	3.11
Savanna	2.74	5.81	3.08
Nama Karoo	2.15	4.69	2.54
Succulent Karoo	1.70	2.21	0.51
Forest	-6.40	-6.40	0.00
Albany Thicket	-0.17	-2.11	-1.94

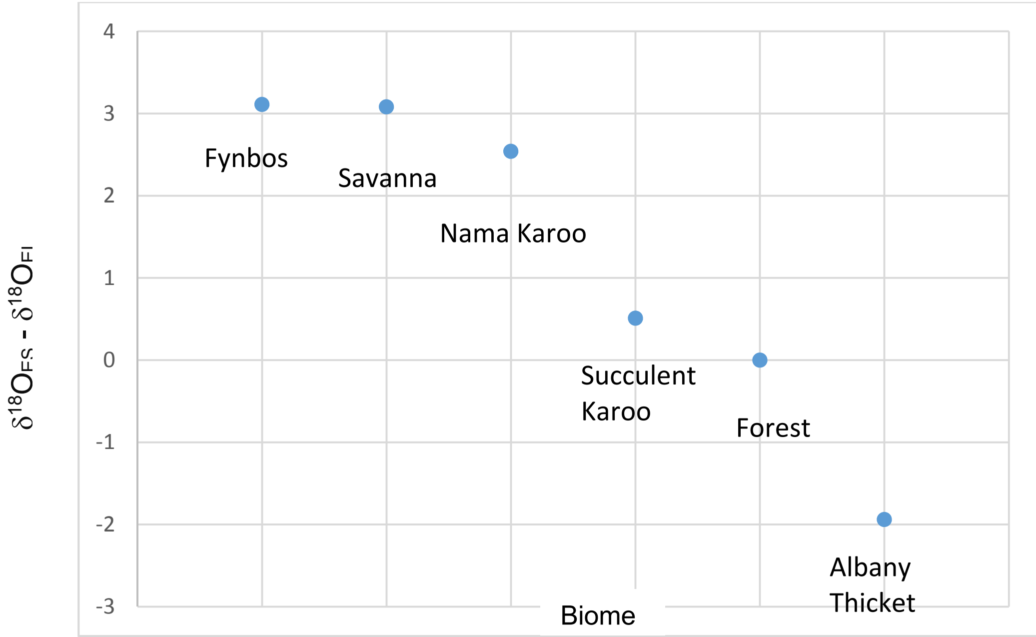

Figure 5. 18 The difference between the $\delta^{18}O_{enamel}$ of water independent (WI) and water dependent (WD) animals for each biome (WI-WD).

5.4.7 $\delta^{18}O_{enamel}$ summary

Browsers have the most positive values in the Savanna biome and the most negative values in the Forest biome. The $\delta^{18}O$ values of browsers and grazers were only significantly different from each other in the Fynbos biome. Mixed feeders had relatively positive $\delta^{18}O_{enamel}$ values.

$\delta^{18}O_{enamel}$ in ungulates showed a significant relationship with all meteorological factors except SAI. The strongest relationships were with MAP (r^2 = 0.60), MAPE (r^2 =0.63), WD (r^2 = 0.64) and MI (r^2 = 0.61). Carnivore $\delta^{18}O$ showed significant correlations (at p<0.05) with MAP, MAPE, SAI, WD and MI but as with $\delta^{13}C$, the r^2 values were low indicating that meteorological factors are not a good predictor of their $\delta^{18}O$. Primate $\delta^{18}O$ did not have strong relationships with meteorological factors.

In general, when compared to more arid environmental contexts, the cooler or comparatively moist biomes demonstrated smaller differences between ES and EI animals. Similarly, the difference in average $\delta^{18}O_{enamel}$ of WD and WI animals increased with increased aridity. There were some exceptions to this pattern, such as in the Fynbos biome. This highly diverse region requires a higher resolution study to understand thoroughly.

5.5 Enamel apatite summary

These data provided a survey of the natural variations of $\delta^{13}C_{enamel}$ and $\delta^{18}O_{enamel}$ in a range of animal species from southwestern South Africa. Browser $\delta^{13}C$ values varied more than expected, showing significant correlations with seven out of nine meteorological factors (the exceptions were RH and SAI). Carnivores were good integrators of environmental signals as their $\delta^{13}C$ values correlated significantly with all the meteorological factors except SAI, while those of primates correlated with none. In most biomes, ES animals were more enriched in ^{18}O than EI ones, and $\delta^{18}O_{enamel}$ for ES animals increased with increased aridity. Animals from the Forest biome were by far the most depleted in ^{18}O, especially ES animals. The Fynbos biome was also less enriched in ^{18}O than other biomes, but not to the same extent as the Forest biome. The $\delta^{18}O_{enamel}$ data also indicated a more significant correlation with meteorological factors when using a single species, particularly in the case of *Tragelaphus oryx* (eland).

Chapter 6: Bone collagen
$\delta^{13}C_{collagen}$ and $\delta^{15}N_{collagen}$

6.1 Introduction

This chapter presents $\delta^{13}C_{collagen}$ and $\delta^{15}N_{collagen}$ measurements from 428 animals (24 ungulate species, two primate species, and 11 carnivore species). Samples originated from all South African biomes that receive a comparatively large proportion of rain in the winter months, as well as adjacent areas. In many cases, the animals analysed were the same individuals for which $\delta^{13}C_{enamel}$ and $\delta^{18}O_{enamel}$ were reported in Chapter 5. However, since both teeth and bone were not available from all individuals, the datasets are not precisely matched. Patterns in $\delta^{13}C_{collagen}$ and $\delta^{15}N_{collagen}$ from different biomes and groups of fauna are explored as well as the relationships of climatic indices with $\delta^{13}C_{collagen}$ and $\delta^{15}N_{collagen}$. Correlations were run between the climatic indices and the $\delta^{13}C_{collagen}$ and $\delta^{15}N_{collagen}$ values. Regressions were carried out in order to express the relationships as linear equations. $\delta^{13}C_{collagen}$ and $\delta^{15}N_{collagen}$ are then compared, and the chapter ends with an exploration of to what extent the current study data set can be used to predict $\delta^{15}N_{collagen}$ values from $\delta^{18}O_{enamel}$ values.

6.2 $\delta^{13}C_{collagen}$

6.2.1 General observations

$\delta^{13}C_{collagen}$ values in this study ranged between -24.8 and -6.9‰ (for individual values, see Appendix 7). Each sample was run in duplicate, and averages reported. As the data were not normally distributed, non-parametric approaches were used. Means and standard deviations are listed in Appendix 8c.

The $\delta^{13}C_{collagen}$ for ungulates (the largest group) ranged from -24.8 to -6.9‰ (median = -18.4‰, n = 251) (Table 6.1). The $\delta^{13}C_{collagen}$ values of carnivores ranged from -20.9‰ to -10.6‰ (median = -17.4‰, n = 32). The $\delta^{13}C_{collagen}$ values of primates ranged from -22.0‰ to -10.9‰ (median = -20.2‰, n = 145).

Table 6. 1 Descriptive statistics for $\delta^{13}C_{collagen}$ (‰) by faunal category.

Type	Feeder type	N	Median	Minimum	Maximum
Carnivore	Carnivore	32	-17.4	-20.9	-10.6
Primate	Omnivore	145	-20.2	-22	-10.9
Ungulate	All	251	-18.4	-24.8	-6.9
	Browser	102	-20.0	-24.8	-14.8
	Grazer	117	-12.3	-22.4	-6.9
	Mixed feeder	19	-19.4	-21.3	-15.3
	Omnivore	13	-20.8	-22.8	-19

The range for $\delta^{13}C_{collagen}$ was largest for the grazing subset (Figure 6.1), while values for omnivores and browsers were at the most negative end of the range, indicating reliance on C_3 resources. Browsers had tightly clustered $\delta^{13}C_{collagen}$ with only 3 outliers (Figure 6.1). While the mixed feeder category was also tightly clustered (ranging from -21.3 to -15.3) the sample size was small (n=19) compared to the browser sample size (n=102). Other categories had larger ranges (between 10.6 and 15.5).

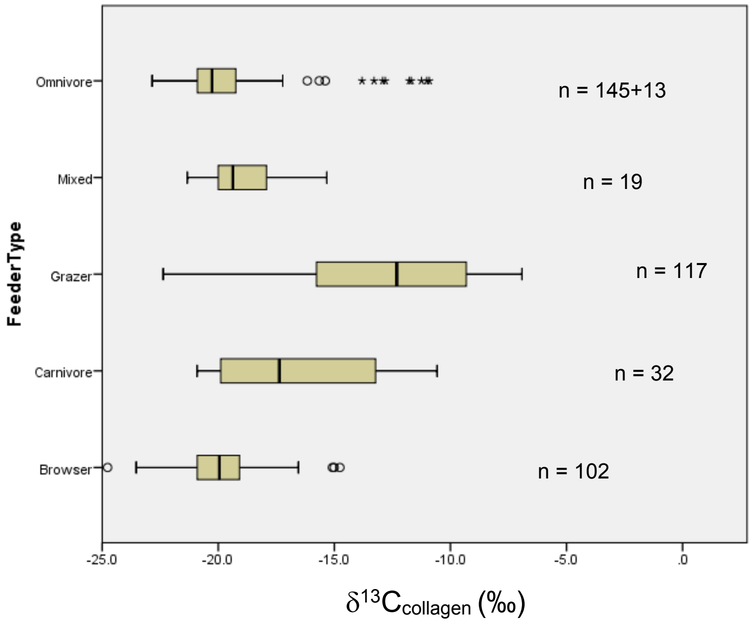

Figure 6. 1 $\delta^{13}C_{collagen}$ (‰) for all biomes by feeder type. Omnivores include primates and omnivorous ungulates. Bold vertical lines indicate the median, with surrounding boxes representing the interquartile range (first quartile to third quartile). The whiskers indicate the range of values that are not outliers. Outliers (values between 1.5 and 3 times the interquartile range away from the median) are indicated by open circles and extreme outliers (values more than 3 times the interquartile range away from the median) are indicated by stars.

6.2.2 Results by feeding preference

6.2.2.1 Ungulates

$\delta^{13}C_{collagen}$ for browsers varied according to vegetation type (Figure 6.2a) (Kruskal-Wallis H (5) =43.17, $p < 0.001$). The highest values occurred in the Albany Thicket (median = -19.3‰), the Nama Karoo (median = -18.6‰) and the Succulent Karoo (median = -19.5‰). Two browsers from the Succulent Karoo had more positive values (-14.8 and -15.0). These two specimens are *Raphicerus campestris* (steenbok) and are the only two browser specimens in this group not to originate from the Anysberg nature reserve (Figure 6.3 illustrates these outliers by their two collection locations). The Forest biome had the lowest values (median = -21.9‰), which were significantly lower than the Savanna ($p = 0.049$), Nama Karoo ($p = 0.001$), Succulent Karoo ($p < 0.001$) and Albany Thicket ($p < 0.001$) biomes. The Fynbos biome also exhibited negative values (median = -21.1‰), which were significantly lower than Albany Thicket ($p = 0.026$). The values for the Succulent Karoo were significantly higher than Fynbos (p = 0.003). Figure 6.3a illustrates the $\delta^{13}C_{collagen}$ results per location from each biome. Most of the Fynbos locations were very negative (green) while the summer rainfall locations (Savanna and Nama Karoo) were less negative (yellow) values.

Among grazers (Figure 6.2b), values from the Fynbos biome were the most negative (median = -20.2‰, n = 14). The Succulent Karoo is also relatively low with a median of -15.8‰ (n = 27). Fynbos and Succulent Karoo biomes were not significantly different from each other ($p = 0.313$) but they were both significantly different from the Savanna ($p < 0.001$ and $p = 0.006$ respectively) and the Albany Thicket biomes ($p < 0.001$ for both) biomes. Figure 6.3b illustrates that $\delta^{13}C$ values were less negative in areas that receive summer rainfall.

Mixed feeders (springbok) were collected from three biomes (Figure 6.2c). Median $\delta^{13}C_{collagen}$ values in the Succulent Karoo and Nama Karoo were -19.3‰ and -19.9‰ respectively, The Savanna had a less negative median of -17.2‰, indicating a slightly larger proportion of C_4 grass and/or CAM plants in the diet. The $\delta^{13}C_{collagen}$ values for mixed feeders seemed similar to the values for browsers, indicating that these animals were mainly browsing, but sample numbers were too small for meaningful statistical comparisons. Figure 6.3c presents the data by individual collection locations. Although there are only four collection points, $\delta^{13}C_{collagen}$ values from the most easterly location (i.e. furthest into the summer rainfall regime) were the least negative.

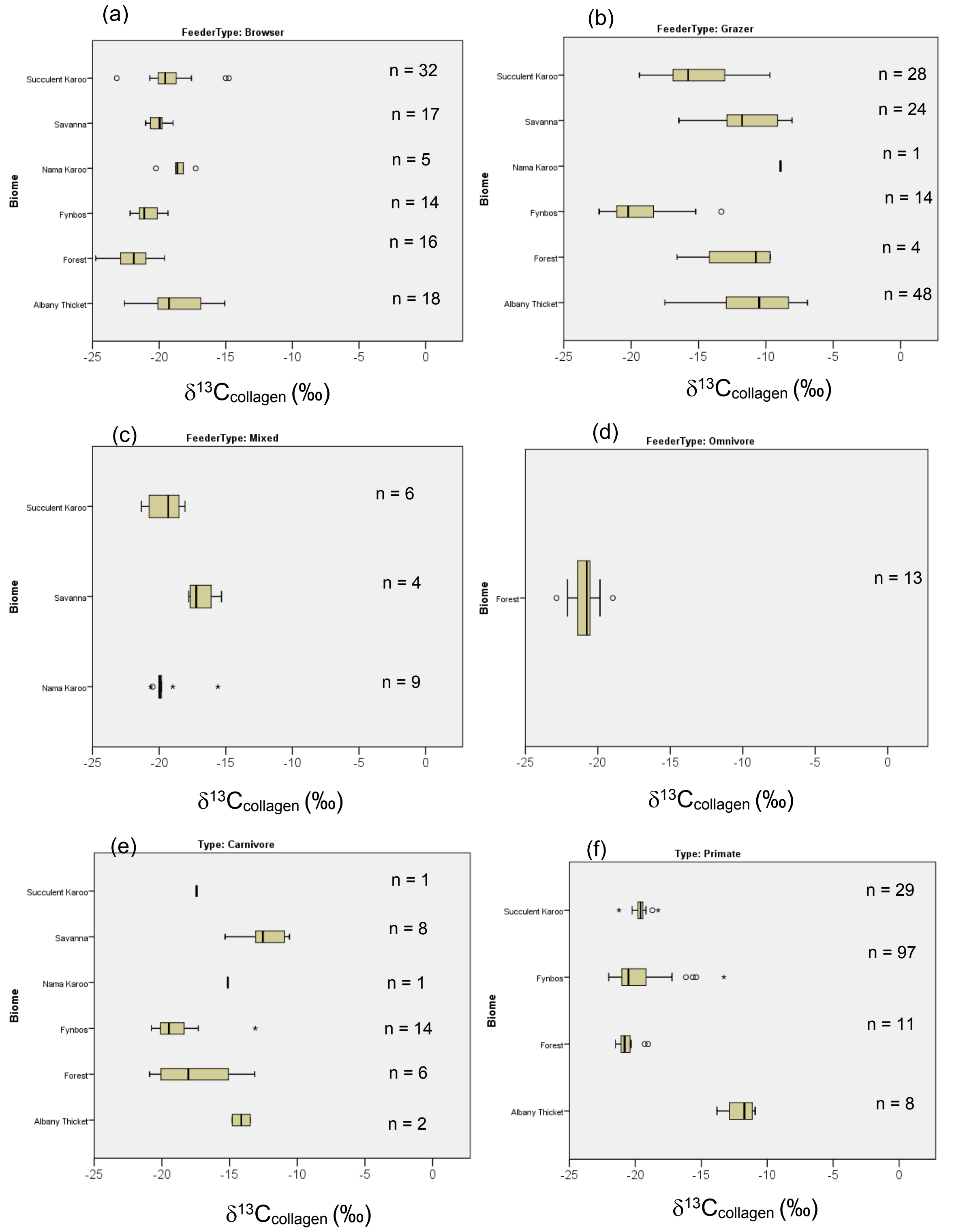

Figure 6. 2 $\delta^{13}C_{collagen}$ (‰) of a) browsers, b) grazers, c) mixed feeders, d) omnivorous ungulates, e) carnivores and f) primates. See legend to Fig. 6.1 for an explanation of the format of the plots.

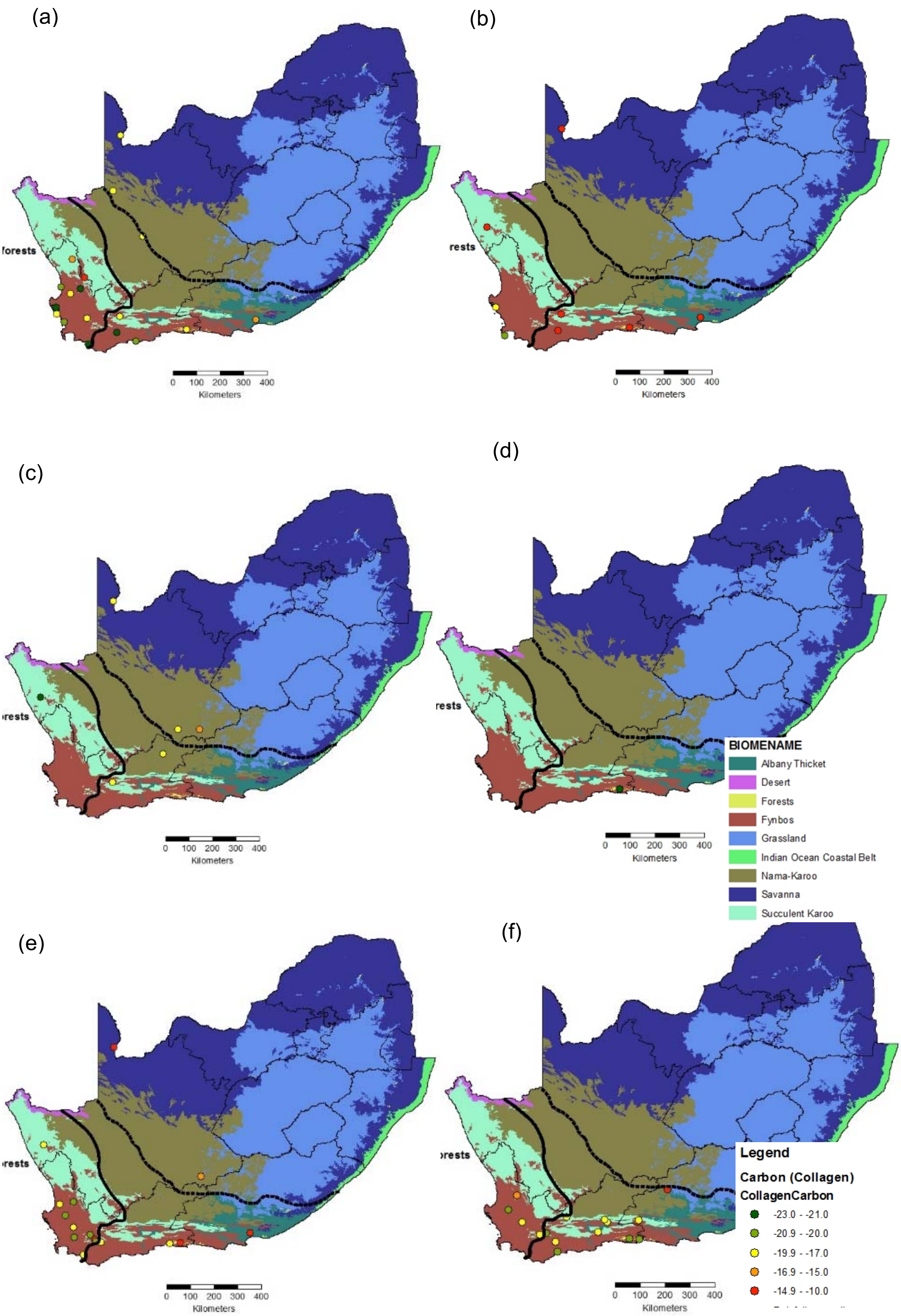

Figure 6. 3 $\delta^{13}C_{collagen}$ (‰) of a) browsers, b) grazers, c) mixed feeders, d) omnivorous ungulates, e) carnivores and f) primates by collection location across the sampled biomes. Circles represent means per collection location. The solid line indicates the approximate extent of the winter rainfall zone, the dotted line indicates the beginning of the summer rainfall zone and the area between the lines indicates the year-round rainfall zone.

Omnivorous ungulates (all bushpigs) were collected from the Forest biome only (Figure 6.2d and Figure 6.3d). The values for the 13 specimens were tightly clustered with a median of -20.8‰. The bushpigs were thus eating only C_3 plants from the cool moist forest environment, and these plants would have been further depleted in ^{13}C due to the wet conditions.

6.2.2.2 Carnivores

For carnivores (Figure 6.2e), the most negative values derive from the Fynbos biome (median = -19.5‰, n = 14) and the Forest biome (median = -18.0‰, n = 6). These two groups were not significantly different (p = 1.000). Albany Thicket and Savanna (the two summer rainfall biomes) had the highest values (-14.1‰, n = 2; and -12.5‰, n = 8, respectively). The Savanna biome has significantly higher values than the Fynbos biome (p=0.001). Savanna is not significantly different to the Forest biome (*p*=0.015).Small sample size precludes comparisons for Succulent Karoo and Nama Karoo. Figure 6.3e represents the $\delta^{13}C$ of individual collection locations, with the highest values occurring in biomes with a higher concentration of C_4 vegetation (Savanna and Albany Thicket).

6.2.2.3 Primates

The primates consisted of chacma baboon (n=146) and two vervet monkeys. Values from the Forest, Fynbos and Succulent Karoo biomes were all very negative (medians -20.8‰, -20.5‰ and -19.6‰ respectively) (Figure 6.2f). Albany Thicket showed less negative values, with the median at -11.7‰. Values from the Forest and Fynbos biomes were similar to each other but significantly lower than the Succulent Karoo ($p < 0.001$ and $p = 0.017$ respectively) and Albany Thicket ($p < 0.001$ and $p < 0.001$ respectively). Values from the Succulent Karoo biome were significantly lower than the Albany Thicket biome ($p = 0.017$). Figure 6.3f indicates the less negative values for Albany Thicket, indicating a substantial proportion of C_4 and/or CAM resources in the diets of primates in this region.

6.2.3 Results by biome

In the Forest biome, values for browsers (median = -21.9‰, n = 16) and omnivores (median = -18.0‰, n = 24) fell on the C_3 end of the range (Figure 6.4a). The median value for carnivores was -20.8‰. As a group carnivores had the highest $\delta^{13}C_{collagen}$ values (-13.1‰, -15.1‰ for the two most positive). There were four grazers: three hippopotami with $\delta^{13}C_{collagen}$ values of -9.7‰, -11.8‰ and -16.6‰, and a buffalo with a with $\delta^{13}C_{collagen}$ value of -9.7‰. There were significant differences between grazers and browsers ($p < 0.001$) and grazers and omnivores ($p = 0.026$), as well as between browsers and carnivores ($p = 0.002$).

For the Fynbos winter rainfall biome, the results were uniform, with medians for the faunal groups ranging from -19.5 to -21.1‰ (Figure 6.4b) indicating that all faunal groups (including grazers) consumed a negligible amount of C_4 grasses. Only browsers and carnivores were significantly different from each other (p = 0.044) (Kruskal-Wallis H (3) = 14.67, p = 0.002). There was no significant difference between browsers and grazers (p =0.094).

In the Succulent Karoo, there were significant differences between $\delta^{13}C_{collagen}$ values of animals with different feeding patterns (Kruskal-Wallis H (4) = 52.78, p < 0.001). The browsers had a median of -19.5‰ (Figure 6.4c). Grazers (median = -15.8‰) exhibited a large range but were significantly less negative than other groups (mixed feeders, p = 0.008; browsers, p < 0.001; and omnivores, p = 0.001) (Figure 6.13). The ranges for omnivores (median = -19.6‰), mixed feeders (median = -19.3‰) and browsers (median = -19.5‰) were similar to each other. These three groups are not significantly different from each other (omnivores and mixed feeders (p=1.000); mixed feeders and browsers (p=1.000); browsers and omnivores (p=1.000).

For the Albany Thicket biome, an environment with both C_3 and C_4 elements, grazers consumed substantially more C_4 than browsers (Figure 6.4d). Grazer $\delta^{13}C_{collagen}$ median was -10.5‰ while browser $\delta^{13}C_{collagen}$ median was -19.3‰. These two groups were significantly different (p < 0.001) (Kruskal-Wallis H (3) = 57.035, p < 0.001). Omnivores (ungulate omnivores and primates) and carnivore values were in between browsers and grazers. There was a significant difference between browsers and omnivores (p = 0.013), but no significant differences between the other animal groupings. It should be noted that the carnivore group comprised only two specimens.

While there were very few samples in the Nama Karoo biome, it is still useful to note the grazer was the most enriched in ^{13}C (at -8.9‰) while the browsers (median -18.6‰) and mixed feeders (median -19.9‰) are much more depleted in ^{13}C (Figure 6.4e). A Kruskal-Wallis test showed no significant differences across the groups (Kruskal-Wallis H (3) = 6.778, p=0.079). A larger sample size would improve confidence in this result.

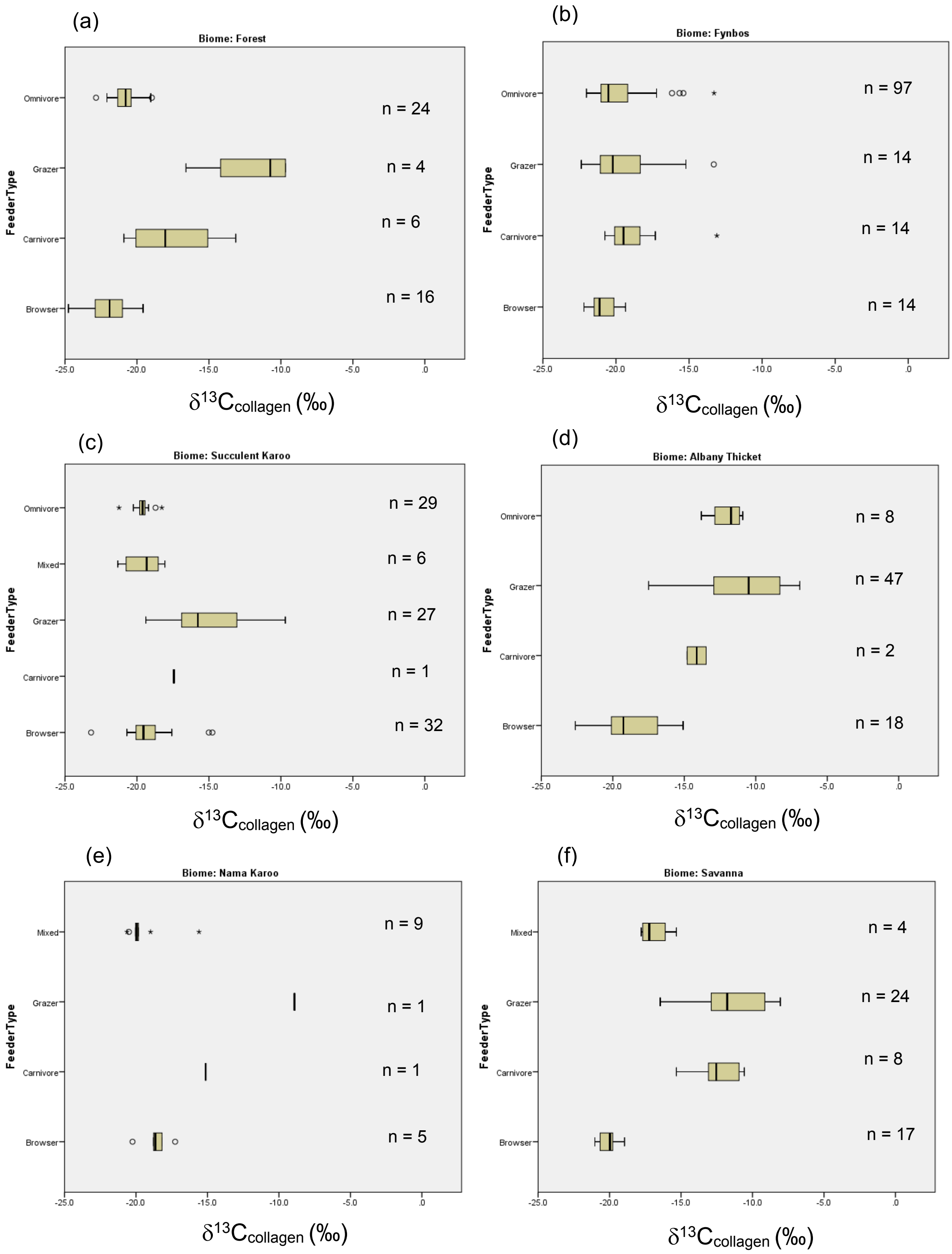

Figure 6. 4 $\delta^{13}C_{collagen}$ (‰) for the a) Forest, b) Fynbos, c), Succulent Karoo, d) Albany Thicket, e) Nama Karoo and f) Savanna biomes by feeder type. See legend to Fig. 6.1 for an explanation of the format of the plots.

In the Savanna biome, there were significant differences between the $\delta^{13}C$ values across feeding types (Kruskal-Wallis H (3) = 39.43, $p < 0.001$). Browsers were the most negative (median = -20.0‰), with mixed feeding species somewhat less negative (median = -17.2‰) indicating a greater reliance on C_4 resources (Figure 6.4f). Grazers (median = -11.8‰) had a large range of $\delta^{13}C$ values (from -8.1 to -16.5‰), which encompassed that of carnivores. Browsers were significantly different from carnivores ($p = 0.001$) and grazers ($p < 0.001$) but not from mixed feeders ($p = 1.000$), though confidence is limited for mixed feeders due to small sample size. Carnivores were also not significantly different from grazers ($p = 1.000$) or mixed feeders ($p = 0.898$).

6.2.4 Relationships between $\delta^{13}C_{collagen}$ and meteorological factors

The next section explores relationships between $\delta^{13}C_{collagen}$ and meteorological variables. In the first instance correlations are run and then regression models.

6.2.4.1 Correlations

The next section explores correlations between $\delta^{13}C_{collagen}$ and meteorological variables. The following table (6.2) provides results of the correlations (Spearman's rho) between $\delta^{13}C_{collagen}$ and all the meteorological factors.

As for $\delta^{13}C_{enamel,}$ the $\delta^{13}C_{collagen}$ for carnivores is the dataset correlated with the largest number (eight out of nine) meteorological factors, with SAI the only exception. This pattern indicates that, as for $\delta^{13}C_{enamel}$, carnivores are an effective integrator of environmental influences on animal $\delta^{13}C$. $\delta^{13}C_{collagen}$ of grazers and mixed feeders are correlated with only three meteorological factors and browsers with five (See Table 6.2). While browsers show significant correlations with a five meteorological factors, the correlation coefficients are much lower than for carnivores, indicating more variance. It is interesting that $\delta^{13}C_{collagen}$ of mixed feeders are significantly correlated with three factors (RH, SAI and WCR), since their $\delta^{13}C_{enamel}$ did not correlate with any meteorological factors. This presumably results from the greater scatter in the $\delta^{13}C_{enamel}$ dataset.

Table 6. 2: Correlation coefficients for $\delta^{13}C_{collagen}$ and meteorological variables from all locations. The number of specimens varies across the rows because not all variables are available for all locations. 'Omnivore' includes ungulate omnivores and primate omnivores. Correlation coefficients are considered significant when $p < 0.05$ (in bold). Mean annual precipitation (MAP), mean annual temperature (MAT), mean annual soil moisture stress (MASMS), mean annual potential evapotranspiration (MAPE), relative humidity (RH), summer aridity index (SAI), winter concentration of rainfall (WCR), moisture index (MI) and water deficit (WD).

Feeder type		MAP	MAT	MASMS	MAPE	RH	SAI	WCR	WD	MI
Browser	Correlation coefficient (r_s)	**-0.379****	0.108	0.190	**0.340****	-0.179	-0.168	**-0.413****	**0.342****	**-0.359****
	Sig. (2-tailed)	0.001	0.582	0.310	0.002	0.129	0.041	0.000	0.002	0.001
	N	102	102	86	102	102	102	102	102	102
Grazer	Correlation coefficient (r_s)	0.138	**0.590****	0.179	-0.131	0.177	**0.569****	**-0.564****	-0.131	0.138
	Sig. (2-tailed)	0.137	0.000	0.057	0.158	0.057	0.000	0.000	0.160	0.137
	N	117	117	113	117	117	117	117	117	117
Mixed	Correlation coefficient (r_s)	-0.036	0.370	0.415	0.369	**-0.462***	**0.462***	**-0.708****	0.205	-0.036
	Sig. (2-tailed)	0.885	0.119	0.077	0.119	0.047	0.047	0.001	0.399	0.885
	N	19	19	19	19	19	19	19	19	19
Omnivore	Correlation coefficient (r_s)	**-0.350****	-0.090	**0.568****	**0.412****	-0.154	0.083	**-0.485****	**0.439****	**-0.419****
	Sig. (2-tailed)	0.000	0.261	0.000	0.000	0.054	0.299	0.000	0.000	0.000
	N	158	158	134	158	158	158	158	158	158
Carnivore	Correlation coefficient (r_s)	**-0.550****	**0.683****	**0.765****	**0.527****	**-0.649****	0.328	**-0.746****	**0.530****	**-0.469****
	Sig. (2-tailed)	0.001	0.000	0.000	0.002	0.000	0.067	0.000	0.002	0.007
	N	32	32	26	32	32	32	32	32	32

**. Correlation is significant at the 0.01 level (2-tailed).

*. Correlation is significant at the 0.05 level (2-tailed).

Following these tests, regression models were run, firstly on the meteorological factors one at a time (simple regression) and secondly on a combination of factors (multiple regression).

6.2.4.2 Simple regression

Univariate regression models were run for the $\delta^{13}C_{collagen}$ and each of the meteorological factors. For ungulates, fixed variables included the feeder type (grazer, browser, mixed feeder or omnivore) and animal size (small, medium, large, extra-large). A summary of the outcome of the regression analysis for ungulates where each of the meteorological factors was tested individually is provided in Table 6.3.

Table 6. 3 Summary outcome of regression models for $\delta^{13}C_{collagen}$ for ungulates against each meteorological factor individually. The adjusted r^2 is modified for the number of predictors in the model. For models with only one predictor, r^2 should suffice, but for consistency r^2 adjusted is reported. B is the unstandardised regression coefficient (the change in the isotope value with a one unit change in meteorological factor); t is the test statistic (used to test whether B is significantly different from zero). *p*-values that are significant at <0.05 are in bold. Mean annual precipitation (MAP), mean annual temperature (MAT), mean annual soil moisture stress (MASMS), mean annual potential evapotranspiration (MAPE), relative humidity (RH), summer aridity index (SAI), winter concentration of rainfall (WCR), moisture index (MI) and water deficit (WD).

					95% Confidence interval			
Met. variables	B	Std. error	t	*p*	Lower bound	Upper bound	r^2	r^2 adj
MAP	-0.001	0.001	-0.673	0.501	-0.003	0.001	0.57	0.56
MAT	1.319	0.249	5.300	**< 0.001**	0.829	1.809	0.61	0.60
MASMS	0.149	0.054	2.751	**0.006**	0.042	0.256	0.53	0.52
MAPE	0.001	0.001	1.010	0.313	-0.001	0.002	0.57	0.56
RH	-0.020	0.019	-1.085	0.279	-0.057	0.016	0.57	0.56
SAI	0.020	0.003	7.294	**< 0.001**	0.014	0.025	0.64	0.63
WCR	-0.071	0.009	-8.048	**< 0.001**	-0.089	-0.054	0.66	0.65
WD	0.000	0.000	0.929	0.354	0.000	0.001	0.57	0.56
MI	-1.876	1.737	-1.080	0.281	-5.297	1.545	0.57	0.56

Correlations with mean annual temperature (MAT), mean annual soil moisture stress (MASMS), summer aridity index (SAI) and winter concentration of rainfall (WCR) were significant for ungulates (Table 6.3). Based on the data available here, the model predicts that with an increase of 1 degree Celsius, the $\delta^{13}C_{collagen}$ value is expected to increase by 1.319‰ (B value). For an increase of 10% in MASMS, the $\delta^{13}C_{collagen}$ value is expected to increase by 1.49‰ (0.149 × 10) (Refer to Table 5.5 for adjustments made to B). The change in SAI is expected to be smaller; a 50 point SAI increase is expected to result in an increase in isotope value by 1.00‰ (0.02 × 50). An increase of 10% in WCR, the isotopic value is expected to decrease by 0.71‰ (0.071 x 10). For these ungulates, the r^2 values ranged between 0.52 (a moderately good fit) to 0.65 (a good fit), depending on the variable. The tables in Appendix 9 provide the outcome of the individual models for each of the meteorological factors.

For carnivores, the regression model indicated a significant linear relationship between $\delta^{13}C_{collagen}$ and all meteorological factors (Table 6.4). However, the r^2 values were low, ranging from 0.21 (p = 0.005) for MI to 0.66 (p < 0.001) for MASMS.

Table 6. 4 Summary outcome of the regression models for $\delta^{13}C_{collagen}$ for carnivores against each meteorological factor individually. The adjusted r^2 is modified for the number of predictors in the model. For models with only one predictor, r^2 should suffice, but for consistency r^2 adjusted is reported. B is the unstandardised regression coefficient (the change in the isotope value with a one unit change in meteorological factor); t is the test statistic (used to test whether B is significantly different from zero). *p*-values that are significant at <0.05 are in bold. Mean annual precipitation (MAP), mean annual temperature (MAT), mean annual soil moisture stress (MASMS), mean annual potential evapotranspiration (MAPE), relative humidity (RH), summer aridity index (SAI), winter concentration of rainfall (WCR), moisture index (MI) and water deficit (WD).

					95% Confidence interval			
Met. variables	B	Std. error	t	*p*	Lower bound	Upper bound	r^2	r^2 adj
MAP	-0.007	0.002	-3.334	**0.002**	-0.011	-0.003	0.27	0.25
MAT	2.235	0.335	6.663	**< 0.001**	1.550	2.920	0.60	0.58
MASMS	0.373	0.053	7.084	**< 0.001**	0.264	0.481	0.68	0.66
MAPE	0.005	0.001	4.579	**< 0.001**	0.003	0.007	0.41	0.39
RH	-0.190	0.034	-5.567	**< 0.001**	-0.260	-0.120	0.51	0.49
SAI	0.020	0.005	3.576	**0.001**	0.008	0.031	0.30	0.28
WCR	-0.084	0.013	-6.521	**< 0.001**	-0.111	-0.058	0.59	0.57
WD	0.003	0.001	4.276	**< 0.001**	0.002	0.004	0.38	0.36
MI	-9.936	3.244	-3.062	**0.005**	-16.562	-3.310	0.24	0.21

For primates, the r^2 values were all near zero, meaning that the variance is large and the values were not adequately described by the model. The results were all significant except for SAI and RH (Table 6.5 below).

Table 6. 5 Summary outcome of the regression models for $\delta^{13}C_{collagen}$ for primates against each meteorological factor individually. The adjusted r^2 is modified for the number of predictors in the model. For models with only one predictor, r^2 should suffice, but for consistency r^2 adjusted is reported. B is the unstandardised regression coefficient (the change in the isotope value with a one unit change in meteorological factor); t is the test statistic (used to test whether B is significantly different from zero). *p*-values that are significant at <0.05 are in bold. Mean annual precipitation (MAP), mean annual temperature (MAT), mean annual soil moisture stress (MASMS), mean annual potential evapotranspiration (MAPE), relative humidity (RH), summer aridity index (SAI), winter concentration of rainfall (WCR), moisture index (MI) and water deficit (WD).

Met.					95% Confidence interval			
variables	B	Std. error	t	*p*	Lower bound	Upper bound	r^2	r^2 adj
MAP	-0.002	0.001	-2.183	**0.031**	-0.004	0.000	0.03	0.03
MAT	0.607	0.248	2.444	**0.016**	0.116	1.098	0.04	0.03
MASMS	0.202	0.050	4.002	**< 0.001**	0.102	0.302	0.11	0.10
MAPE	0.002	0.001	2.167	**0.032**	0.000	0.003	0.03	0.03
RH	0.014	0.024	0.597	0.551	-0.033	0.062	0.00	0.00
SAI	0.003	0.002	1.412	0.160	-0.001	0.008	0.01	0.01
WCR	-0.037	0.008	-4.412	**< 0.001**	-0.054	-0.021	0.12	0.11
WD	0.001	0.000	2.222	**0.028**	0.000	0.002	0.03	0.03
MI	-3.871	1.534	-2.523	**0.013**	-6.904	-0.839	0.04	0.04

6.2.4.3 Multiple regression

The approach employed in this study to identify a 'best model' in the presence of multicollinearity was described in Chapter 4. In this case, the selection process resulted in

MAPE, SAI and WCR being included in the model. The summary is reported below in Table 6.6.

Table 6. 6 The output of the ungulate 'best fit' model using mean annual potential evapotranspiration (MAPE), summer aridity index (SAI) and winter concentration of rainfall (WCR). r^2 = 0.691 (Adjusted r^2= 0.680).

Parameter	B	Std. error	t	*p*	95% Confidence interval	
					Lower bound	Upper bound
Intercept	-12.286	2.095	-5.864	< 0.001	-16.412	-8.159
[FeederType=Browser]	0.348	0.972	0.358	0.721	-1.566	2.261
[FeederType=Grazer]	8.192	0.985	8.316	< 0.001	6.252	10.133
[FeederType=Mixed]	4.035	1.142	3.535	< 0.001	1.787	6.284
[FeederType=Omnivore]	0					
[Size=Extra large]	-1.746	1.239	-1.409	0.160	-4.186	0.695
[Size=Large]	-2.376	0.613	-3.878	< 0.001	-3.583	-1.169
[Size=Medium]	-3.585	0.803	-4.463	< 0.001	-5.168	-2.003
[Size=Small]	0					
MAPE	-0.002	0.001	-3.613	< 0.001	-0.003	-0.001
WCR	-0.078	0.013	-6.059	< 0.001	-0.104	-0.053
SAI	0.008	0.003	2.505	0.013	0.002	0.014

The adjusted r^2 was high (0.68) and was similar to the r^2 from the model for the individual meteorological factors (e.g. WCR r^2 = 0.65).

For carnivores, the regression model using the combination of MAPE, WCR and SAI (Table 6.7) was not significant, and the model indicated that using WCR on its own would be more suitable (significance p <0.024).

Table 6. 7 The output of the carnivore 'best fit' model using mean annual potential evapotranspiration (MAPE), winter concentration of rainfall (WCR) and summer aridity index (SAI). r^2 = 0.639 (Adjusted r^2 = 0.600).

Parameter	B	Std. error	t	*p*	95% Confidence interval	
					Lower bound	Upper bound
Intercept	-17.770	4.146	-4.286	< 0.001	-26.262	-9.277
MAPE	0.002	0.001	1.704	0.099	0.000	0.004
WCR	-0.069	0.029	-2.378	0.024	-0.129	-0.010
SAI	-0.001	0.008	-0.142	0.888	-0.017	0.015

For primates, only WCR was significant and the r^2 value was low (0.108). There was no benefit in adding the other two meteorological factors (Table 6.8).

Table 6. 8 The output of the primate 'best fit' model using mean annual potential evapotranspiration (MAPE), winter concentration of rainfall (WCR) and summer aridity index (SAI). r^2 = 0.127 (Adjusted r^2 = 0.108).

Parameter	B	Std. error	t	*p*	95% Confidence interval Lower bound	Upper bound
Intercept	-19.124	3.060	-6.250	< 0.001	-25.172	-13.075
MAPE	0.001	0.001	0.640	0.523	-0.002	0.003
WCR	-0.036	0.014	-2.600	0.010	-0.063	-0.009
SAI	0.000	0.004	-0.093	0.926	-0.008	0.007

6.2.4.4 Regression models by specific subsets

A regression model was applied, focussing on individual species, to determine the extent to which a more appropriate model could be identified. This process was an attempt to eliminate variation due to the grouping of different species. The species found in several biomes were the red hartebeest and eland. Since one is a grazer (the red hartebeest) and the other a browser (the eland), they make a useful comparison.

Red hartebeest was significantly correlated with MAP, MAT and SAI, although only SAI had a high r^2 value (Table 6.8). The eland was significantly correlated with MASMS and RH, although in both cases with low r^2 values (Table 6.9). The regression using $\delta^{13}C_{collagen}$ provided a much more interesting result than that using $\delta^{13}C_{enamel}$, particularly for the red hartebeest. There were strong correlations with both SAI and WCR (adjusted r^2 values of 0.63 and -0.63, respectively).

Table 6. 9 r^2 values (r^2 adjusted in brackets) of the relationship between the $\delta^{13}C_{collagen}$ value and each of the meteorological factors for the two species (red hartebeest and eland) for which data is available at multiple sites. **. Correlation is significant at the 0.01 level (2-tailed). *. Correlation is significant at the 0.05 level (2-tailed).

	Red hartebeest (grazer)	Eland (browser)
MAP	**0.11 (0.08)***	0.04 (0.00)
MAT	**0.26 (0.24)****	0.03 (0.01)
MASMS	0.09 (0.06)	**0.24 (0.21)***
MAPE	0.01 (-0.02)	0.11 (0.07)
RH	0.03 (0.004)	**0.18 (0.15)***
SAI	**0.62 (0.61)****	0.00 (0.04)
WCR	-0.63 (-0.62)	0.04 (0.00)
WD	0.03 (-0.00)	0.09 (0.05)
MI	0.09 (0.07)	0.03 (0.01)

6.2.5 $\delta^{13}C_{collagen}$ Summary

$\delta^{13}C_{collagen}$ values for all groups of animals (including browsers) differed across biomes. It is interesting that browsers also varied across biomes as this could potentially be used as an environmental proxy. $\delta^{13}C_{collagen}$ of carnivores were highly correlated with all meteorological factors (except SAI) while those of ungulates correlated best with MAT, MASMS, SAI and WCR. $\delta^{13}C_{collagen}$ of primates was poorly correlated with meteorological factors, showing low r^2 values. Complex regression models that incorporate multiple meteorological factors did not add value, since the r^2 values for these complex models did not show significant improvement compared with the r^2 values for models based on individual meteorological factors.

6.3 $\delta^{15}N_{collagen}$

6.3.1 General observations

The 428 bone collagen samples yielded $\delta^{15}N_{collagen}$ values ranging between 1.8‰ and 17.2‰. Appendix 7 lists the $\delta^{15}N_{collagen}$ values for individual specimens, along with the $\delta^{13}C_{collagen}$ values. As the data were non-normally distributed, non-parametric approaches were used and medians were presented (means and standard deviations are given in Appendix 8d). $\delta^{15}N_{collagen}$ values for ungulates (the largest group) ranged between 1.8‰ and 17.2‰ (median = 10.5‰, n = 251). $\delta^{15}N_{collagen}$ values of carnivores ranged between 5.2‰ and 15.2‰ (median = 11.1‰, n = 32), while those of primates ranged between 3.5‰ and 14.3‰ (median = 6.1‰, n = 145). Table 6.10 summarises the descriptive statistics for each grouping for all biomes combined.

Table 6. 10 Descriptive statistics for all $\delta^{15}N_{collagen}$ (‰) by faunal category.

Type	Feeder type	N	Median	Minimum	Maximum
Carnivore	Carnivore	32	11.1	5.2	15.2
Primate	Omnivore	145	6.1	3.5	14.3
Ungulate	All	251	10.5	1.8	17.2
	Browser	102	10.1	1.8	17.2
	Grazer	117	10.8	4.7	15.4
	Mixed feeder	19	11.5	9.3	13
	Omnivore	13	6.3	4.4	8.7

Grazers had the highest $\delta^{15}N_{collagen}$ median of all groups (10.8‰, n = 117) (Kruskal-Wallis H (4) = 171.67, p<0.001) (Table 6.9, Figure 6.5). At this high level overview, the browsers were significantly different from the grazers (p = 0.013). Carnivores were significantly more enriched than browsers (p = 0.020) and omnivores (p < 0.001). In comparison, browsers and mixed feeders were somewhat less enriched in ^{15}N (browsers: 10.1‰, n = 102; mixed: 11.5‰, n = 19). Omnivorous ungulates had the lowest $\delta^{15}N_{collagen}$ (median 6.3 ‰, n = 13). The omnivorous species were significantly less enriched than browsers (p = 0.004), grazers (p < 0.001) and mixed feeders (p < 0.001).

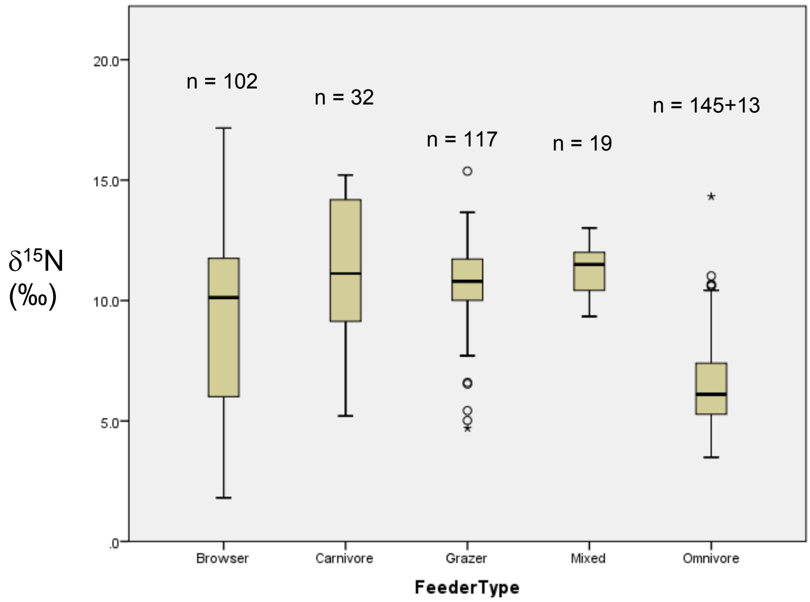

Figure 6. 5 $\delta^{15}N_{collagen}$ (‰) for all biomes by feeder type. (‰) for all biomes by feeder type. See legend to Omnivores include primates (n=146) and omnivorous ungulates (n=14). Bold horizontal lines indicate the median, with surrounding boxes representing the interquartile range (first quartile to third quartile). The whiskers indicate the range of values that are not outliers. Outliers (values between 1.5 and 3 times the interquartile range away from the median) are indicated by open circles and extreme outliers (values more than 3 times the interquartile range away from the median) are indicated by stars.

6.3.2 Results by feeding preference across biome

6.3.2.1 Ungulates

To investigate possible patterns of differentiation in $\delta^{15}N_{collagen}$, ungulates were divided into groups based on diet preference. There were significant differences between the values for browsers from different biomes (Kruskal-Wallis H (5) = 35.08, p < 0.001). The three biomes with summer rainfall (Albany Thicket, Nama Karoo and Savanna) had positive $\delta^{15}N_{collagen}$ medians (11.4‰, 10.1‰ and 10.3‰ respectively) (Figure 6.6a). The winter rainfall biomes, Fynbos and Succulent Karoo, had the largest range of $\delta^{15}N_{collagen}$ values, though Succulent Karoo had a similar median (10.9‰) to Albany Thicket, Nama Karoo and Savanna. $\delta^{15}N_{collagen}$ values from the cool, moist Forest biome were the lowest (median = 3.7‰, n = 16) and were significantly different from Savanna (p = 0.001), Succulent Karoo (p < 0.001) and the Albany Thicket (p < 0.001). Figure 6.7a maps the data by collection location and highlights the range of Fynbos values.

There were also significant differences between grazers from different biomes (Kruskal-Wallis H (5) = 16.59, p = 0.005). The Forest biome had the lowest $\delta^{15}N_{collagen}$ median (median = 8.8‰, n = 4) (Figure 6.6b), while Albany Thicket had the highest (median = 11.2‰, n = 47). Only Savanna and Albany Thicket were significantly different from each other (p = 0.040). Since the sample from the Forest biome comprises few grazers (three hippos and one buffalo), a larger sample size is needed to confirm this pattern for this region, as well as to establish a pattern for the Nama Karoo. Figure 6.7b illustrates the data by collection location.

The mixed feeding species (*springbok*) (Figures 6.6c, 6.7c) had similar $\delta^{15}N_{collagen}$ across biomes. The differences are not statistically significant (Kruskal-Wallis H (2) = 3.017, p = 0.221), although a larger sample size would be needed to confirm this finding.

Omnivorous ungulates (bushpigs) were collected only from the Forest biome (Figures 6.6d, 6.7d. Their low $\delta^{15}N_{collagen}$ (median = 6.3‰, n = 13) was not quite as low as the values for browsers (3.7‰, n = 16) (p = 0.004).

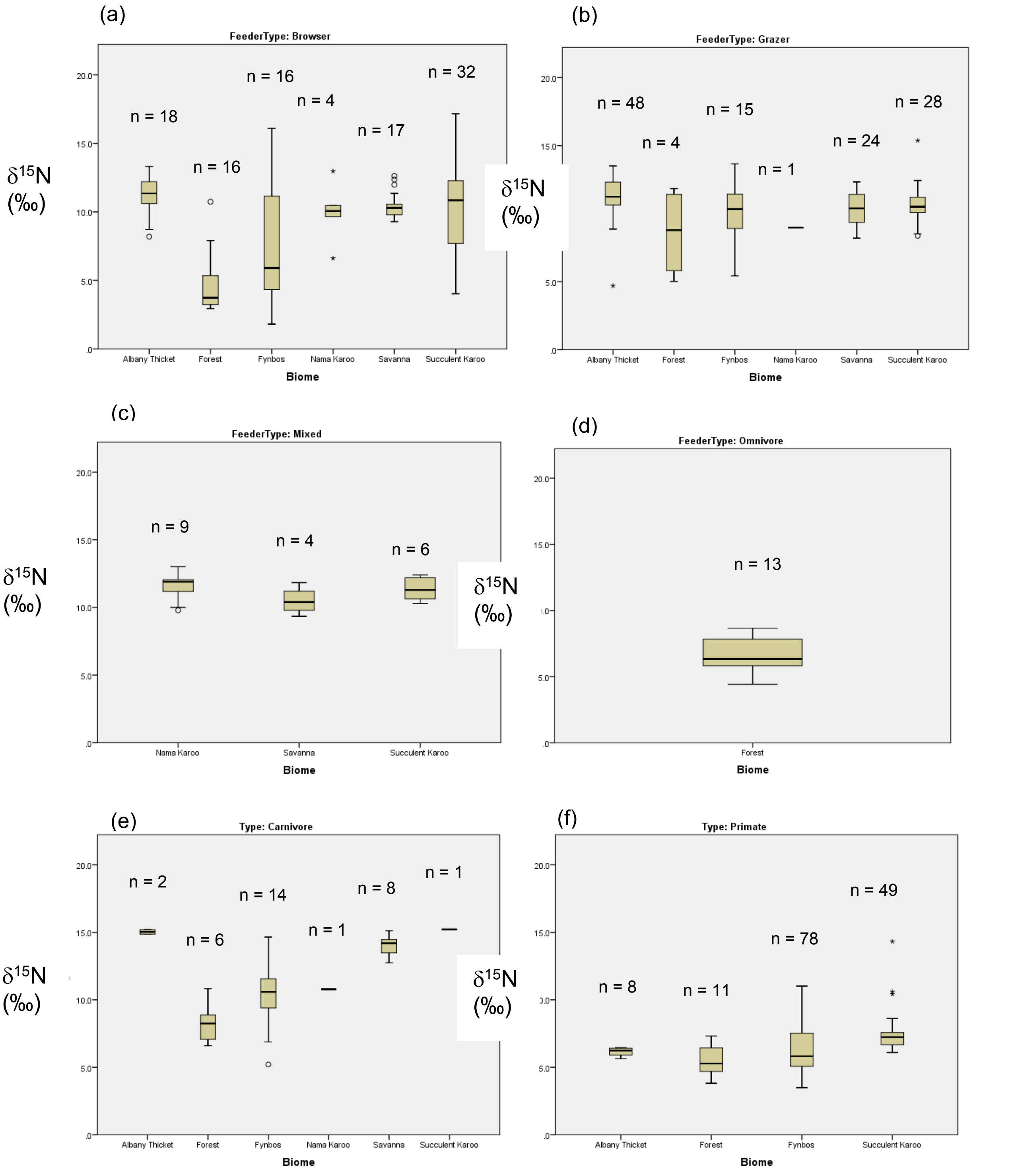

Figure 6. 6 $\delta^{15}N_{collagen}$ (‰) of a) browsers, b) grazers, c) mixed feeders, d) omnivorous ungulates, e) carnivores and f) primates. See legend to Fig. 6.5 for an explanation of the format of the plots.

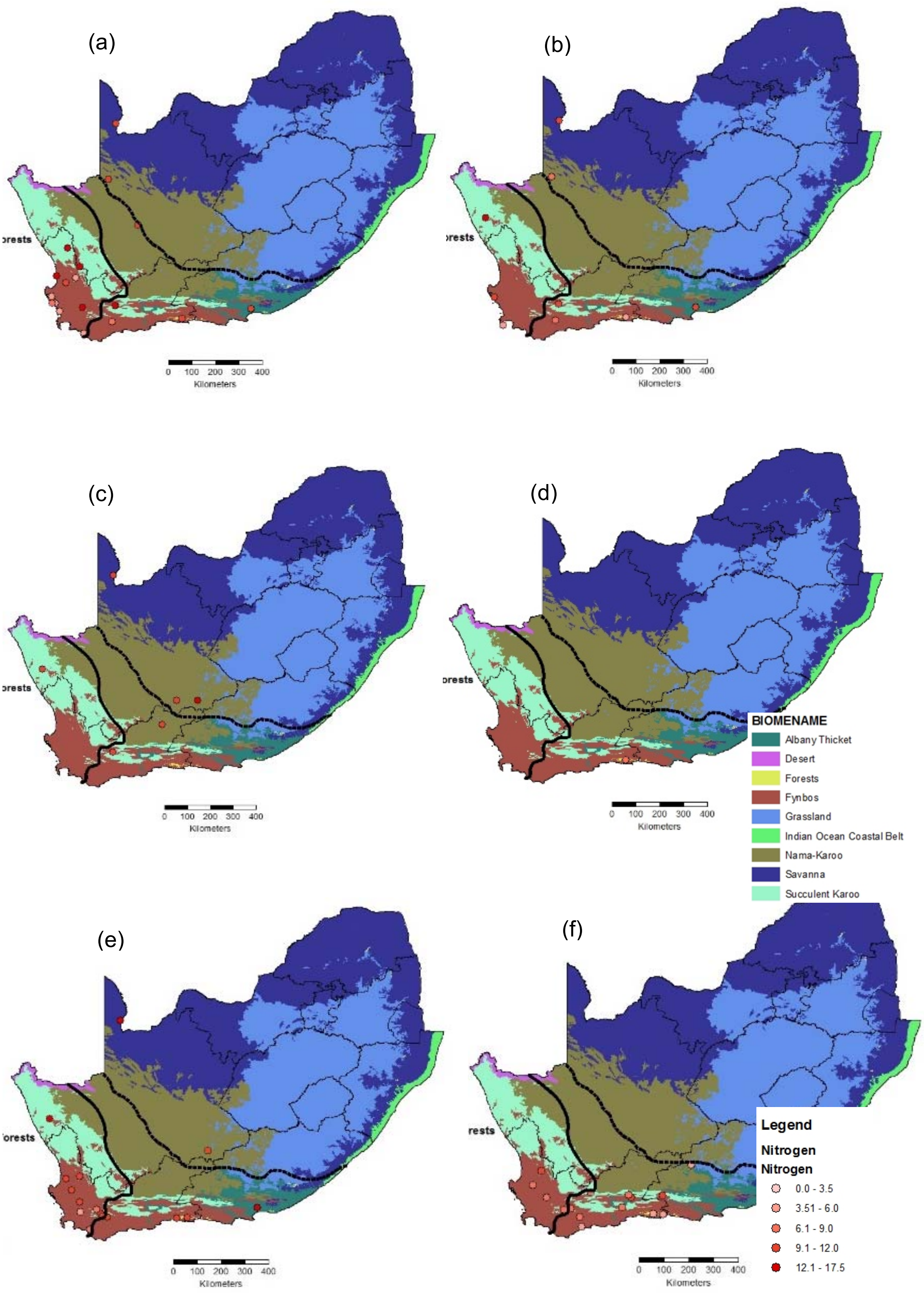

Figure 6. 7 $\delta^{15}N_{collagen}$ (‰) of a) browsers, b) grazers, c) mixed feeders, d) omnivorous ungulates, e) carnivores and f) primates by collection location across the sampled biomes. Circles represent means per collection location. The solid line indicates the approximate extent of the winter rainfall zone, the dotted line indicates the beginning of the summer rainfall zone and the area between the lines indicates the year-round rainfall zone.

6.3.2.2 Carnivores

$\delta^{15}N_{collagen}$ values for carnivores from different biomes were significantly different (Kruskal-Wallis H (5) = 21.39, p = 0.001). Values from the Forest biome were lowest (median = 8.2‰, n = 6), while those from the Albany Thicket (median = 15.0‰, n = 2) and Succulent Karoo (a single observation at 15.2‰) were highest (Figures 6.6e, 6.7e). Values from the Savanna biome were also high (mean = 14.2‰, n = 8). Values from the Fynbos biome varied. The Forest biome was found to be significantly lower from Savanna (p = 0.005) and Albany Thicket biomes (p = 0.038). Differences between the other biomes were not significant (p-values range from 0.204 to 1.000).

6.3.2.3 Primates

$\delta^{15}N_{collagen}$ values for primates (144 chacma baboon and two vervet monkeys) were significantly different between biomes (Kruskal-Wallis H (3) = 27.76, $p < 0.001$). Samples from the Forest biome had the lowest median (5.3‰, n = 11) while those from the Succulent Karoo had the highest (median = 7.2‰, n = 49) (Figures 6.6f, 6.7f). These two were significantly different ($p < 0.001$). The Forest biome was also found to be significantly different from the Fynbos biome ($p < 0.001$).

6.3.2.4 Summary

The most striking feature of the $\delta^{15}N_{collagen}$ dataset was that animals (other than grazers) from the Forest biome had markedly lower $\delta^{15}N_{collagen}$ values than animals from other biomes. A similar pattern may have emerged for grazers had the sample size in the Forest biome been larger. For the $\delta^{15}N_{collagen}$ data set, browsers were more clearly different between biomes than grazers. For browsers, the within-biome variation was high in the two winter rainfall biomes – Fynbos and Succulent Karoo.

6.3.3 Results by isotopic sensitivity to environmental aridity

The following section investigates the extent to which the $\delta^{15}N_{collagen}$ differed between evaporation sensitive (ES) and evaporation insensitive (EI) species. The same analysis was conducted comparing animals that are dependent on drinking water (water dependent - WD) and those that are not as water dependent (water independent - WI). The difference between these two groups is explained in Section 4.5.

Figure 6.8 shows boxplots for ES ungulates (Figure 6.8a) from the various biomes compared with WI ungulates (Figure 6.8b). The patterns were similar. In both cases, values from the Forest biome were significantly lower than all biomes except for the Fynbos biome (Table 6.10). The Fynbos biome was also statistically significantly lower from several biomes (Succulent Karoo; Albany Thicket and Nama Karoo).

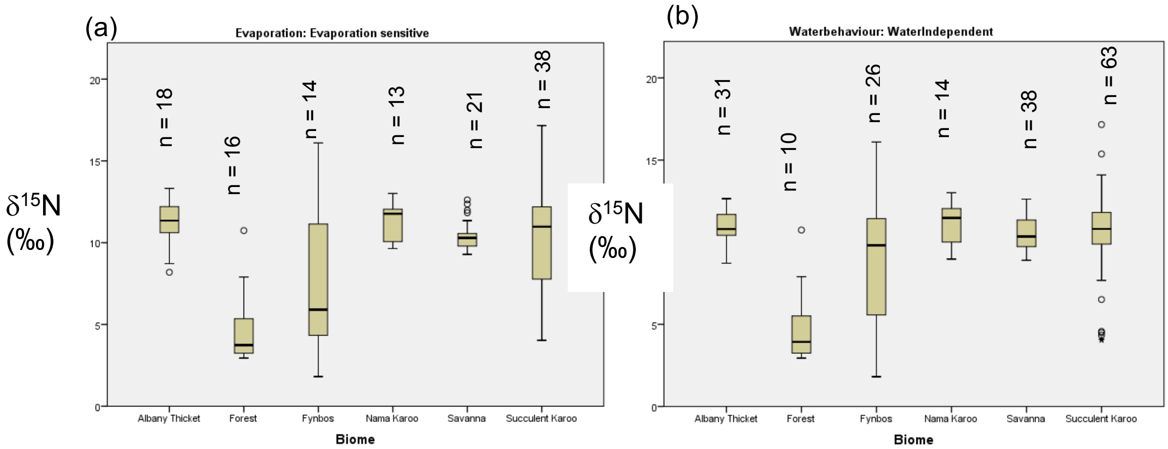

Figure 6. 8 $\delta^{15}N_{collagen}$ (‰) of (a) evaporation sensitive and (b) water independent ungulate species. See legend to Fig. 6.5 for an explanation of the format of the plots.

Table 6. 11 Significance values for posthoc pairwise tests for a) evaporation sensitive and b) water independent ungulate species.

(a)

Sample1-Sample2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj.Sig.
Forest-Fynbos	-27.402	12.730	-2.153	.031	.470
Forest-Savanna	-45.259	11.543	-3.921	.000	.001
Forest-Succulent Karoo	-52.135	10.366	-5.029	.000	.000
Forest-Albany Thicket	61.799	11.952	5.171	.000	.000
Forest-Nama Karoo	-62.688	12.988	-4.826	.000	.000
Fynbos-Savanna	-17.857	12.002	-1.488	.137	1.000
Fynbos-Succulent Karoo	-24.733	10.875	-2.274	.023	.344
Fynbos-Albany Thicket	34.397	12.395	2.775	.006	.083
Fynbos-Nama Karoo	-35.286	13.398	-2.634	.008	.127
Savanna-Succulent Karoo	-6.876	9.458	-.727	.467	1.000
Savanna-Albany Thicket	16.540	11.173	1.480	.139	1.000
Savanna-Nama Karoo	17.429	12.276	1.420	.156	1.000
Succulent Karoo-Albany Thicket	9.664	9.953	.971	.332	1.000
Succulent Karoo-Nama Karoo	10.553	11.177	.944	.345	1.000
Albany Thicket-Nama Karoo	-.889	12.661	-.070	.944	1.000

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.
Asymptotic significances (2-sided tests) are displayed. The significance level is .05.

(b)

Sample1-Sample2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj.Sig.
Forest-Fynbos	-54.104	19.603	-2.760	.006	.087
Forest-Savanna	-66.700	18.724	-3.562	.000	.006
Forest-Succulent Karoo	-80.331	17.933	-4.480	.000	.000
Forest-Albany Thicket	86.966	19.159	4.539	.000	.000
Forest-Nama Karoo	-93.271	21.812	-4.276	.000	.000
Fynbos-Savanna	-12.596	13.408	-.939	.348	1.000
Fynbos-Succulent Karoo	-26.227	12.280	-2.136	.033	.490
Fynbos-Albany Thicket	32.862	14.010	2.346	.019	.285
Fynbos-Nama Karoo	-39.168	17.464	-2.243	.025	.374
Savanna-Succulent Karoo	-13.631	10.821	-1.260	.208	1.000
Savanna-Albany Thicket	20.266	12.750	1.589	.112	1.000
Savanna-Nama Karoo	26.571	16.471	1.613	.107	1.000
Succulent Karoo-Albany Thicket	6.635	11.558	.574	.566	1.000
Succulent Karoo-Nama Karoo	12.940	15.566	.831	.406	1.000
Albany Thicket-Nama Karoo	-6.305	16.964	-.372	.710	1.000

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.
Asymptotic significances (2-sided tests) are displayed. The significance level is .05.

For EI animals (Figure 6.9a), Albany Thicket and Savanna were positive (medians of 11.1‰ and 10.4‰ respectively). Fynbos and Succulent Karoo were also positive (Fynbos median = 10.3‰, n = 14; Succulent Karoo median = 10.5‰, n = 27), while Forest (6.0‰) and Nama Karoo (7.8‰) medians were less positive. Forest biome was significantly different from each of the following biomes: Savanna ($p = 0.006$); Succulent Karoo ($p = 0.001$); Albany Thicket ($p < 0.001$) (Kruskal-Wallis H (5) = 49.99, $p < 0.001$). In the case of WD ungulates (Figure 6.9b), the only significant difference was between the Forest biome and the Albany Thicket biome ($p < 0.001$). The sample size may be too small to confirm differences in other biomes.

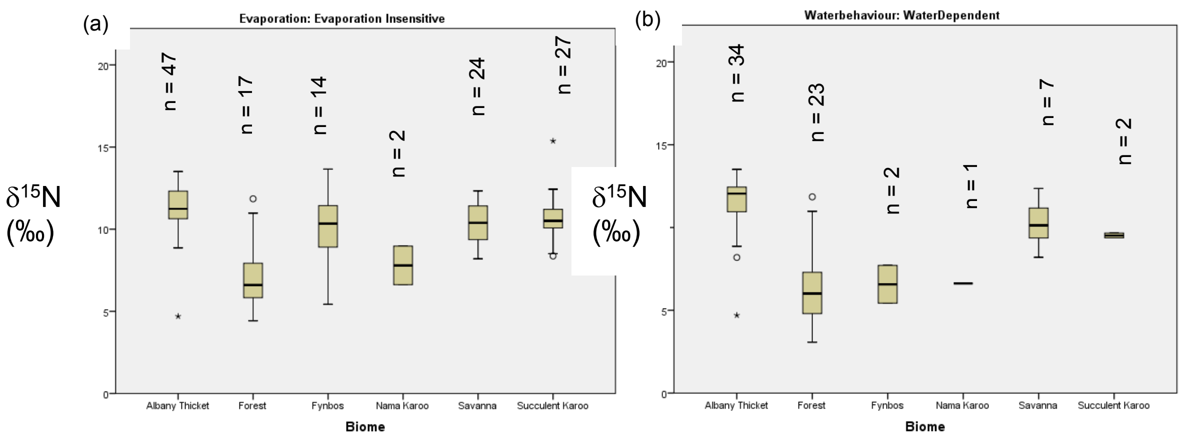

Figure 6. 9 $\delta^{15}N_{collagen}$ (‰) of a) evaporation insensitive and b) water dependent ungulate species. Bold horizontal lines indicate the median, with surrounding boxes representing the interquartile range (first quartile to third quartile). The whiskers indicate the range of values that are not outliers. Outliers (values of between 1.5 and 3 more than the interquartile range) are indicated by an open circle and extreme outliers (values more than 3 times the interquartile range away from the median) are indicated by a solid star.

Table 6. 12 Significance values for posthoc pairwise tests for a) EI ungulates and b) WD ungulates.

(a)

Sample1-Sample2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj.Sig.
Forest-Nama Karoo	-.412	20.377	-.015	.988	1.000
Forest-Fynbos	-37.947	13.700	-2.770	.006	.084
Forest-Savanna	-41.412	12.033	-3.441	.001	.009
Forest-Succulent Karoo	-47.615	11.753	-4.051	.000	.001
Forest-Albany Thicket	66.752	10.743	6.213	.000	.000
Nama Karoo-Fynbos	37.536	28.695	1.308	.191	1.000
Nama Karoo-Savanna	-41.000	27.938	-1.468	.142	1.000
Nama Karoo-Succulent Karoo	-47.204	27.818	-1.697	.090	1.000
Nama Karoo-Albany Thicket	66.340	27.407	2.421	.015	.232
Fynbos-Savanna	-3.464	12.766	-.271	.786	1.000
Fynbos-Succulent Karoo	-9.668	12.502	-.773	.439	1.000
Fynbos-Albany Thicket	28.805	11.558	2.492	.013	.190
Savanna-Succulent Karoo	-6.204	10.649	-.583	.560	1.000
Savanna-Albany Thicket	25.340	9.524	2.661	.008	.117
Succulent Karoo-Albany Thicket	19.137	9.167	2.088	.037	.552

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.
Asymptotic significances (2-sided tests) are displayed. The significance level is .05.

(b)

Sample1-Sample2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj.Sig.
Fynbos-Forest	.196	14.790	.013	.989	1.000
Fynbos-Nama Karoo	-3.500	24.571	-.142	.887	1.000
Fynbos-Succulent Karoo	-15.500	20.062	-.773	.440	1.000
Fynbos-Savanna	-21.786	16.085	-1.354	.176	1.000
Fynbos-Albany Thicket	33.941	14.597	2.325	.020	.301
Forest-Nama Karoo	-3.304	20.493	-.161	.872	1.000
Forest-Succulent Karoo	-15.304	14.790	-1.035	.301	1.000
Forest-Savanna	-21.590	8.660	-2.493	.013	.190
Forest-Albany Thicket	33.746	5.416	6.230	.000	.000
Nama Karoo-Succulent Karoo	-12.000	24.571	-.488	.625	1.000
Nama Karoo-Savanna	-18.286	21.447	-.853	.394	1.000
Nama Karoo-Albany Thicket	30.441	20.355	1.496	.135	1.000
Succulent Karoo-Savanna	6.286	16.085	.391	.696	1.000
Succulent Karoo-Albany Thicket	18.441	14.597	1.263	.206	1.000
Savanna-Albany Thicket	12.155	8.327	1.460	.144	1.000

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.
Asymptotic significances (2-sided tests) are displayed. The significance level is .05.

When comparing biomes (Figure 6.10), Albany Thicket, Savanna, Fynbos and Succulent Karoo biome values for both ES and EI were not significantly different (Mann-Whitney (Z = 405, p = 0.792); (Z = 266.5, p = 0.741); (Z = 58, p = 0.069); (Z = 546, p = 0.660) respectively). The largest differentiation between ES and EI animals was in the Nama Karoo biome, although the numbers sampled were low (Mann-Whitney Z = 26, p = 0.019). There was also a significant difference between ES and EI animals in the Forest biome (Mann-Whitney Z = -3.387, p < 0.001). When the animals were separated by WD and WI behaviours (Figure 6.11), there was no differentiation between the two groups in five out of the six biomes (Forest, Fynbos, Nama

Karoo, Savanna and Succulent Karoo) (Figure 6.9b). For Albany Thicket, WD $\delta^{15}N_{collagen}$ was significantly higher than WI $\delta^{15}N_{collagen}$ (Mann-Whitney Z = -2.909, p = 0.004).

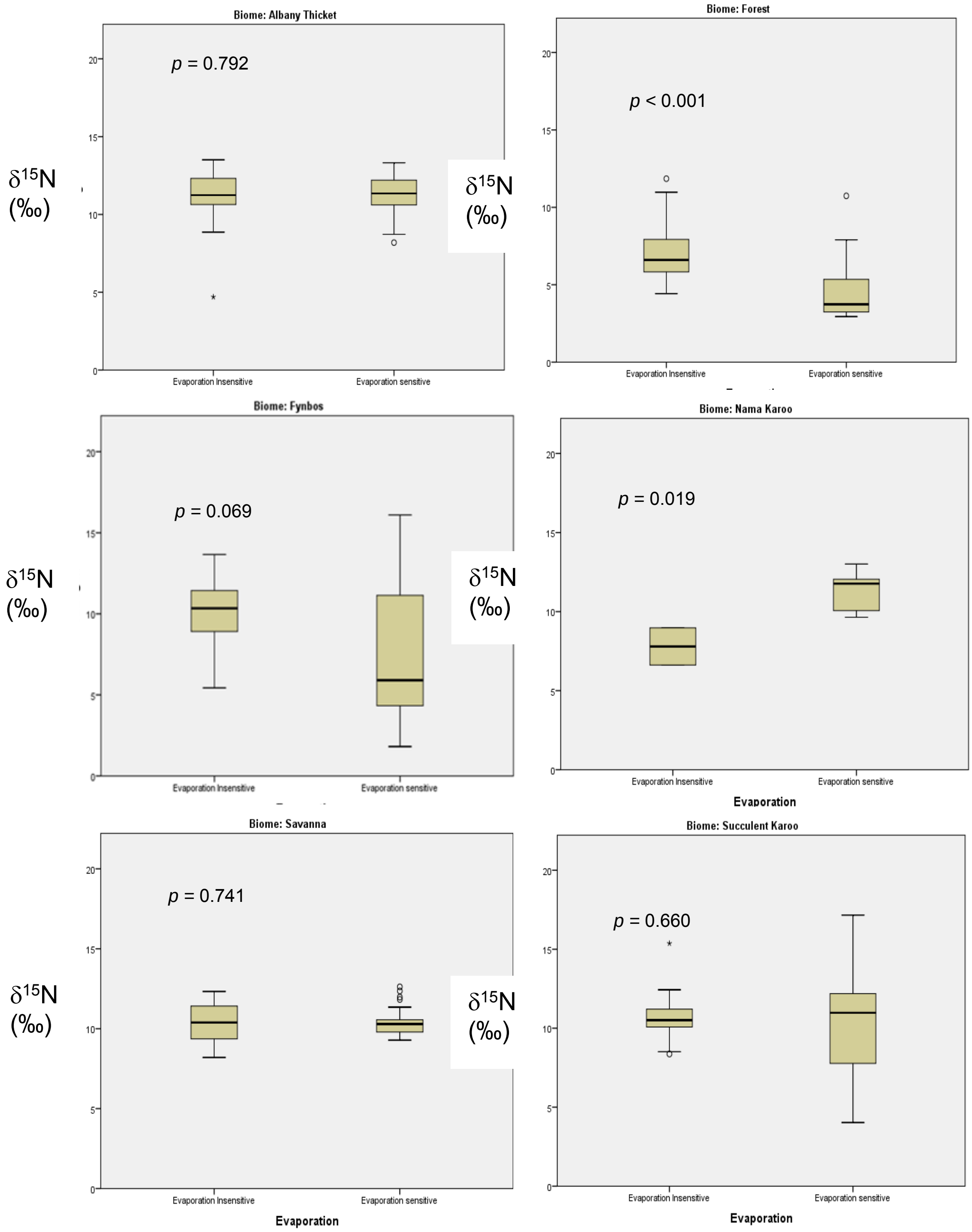

Figure 6. 10 Comparison of $\delta^{15}N_{collagen}$ (‰) of evaporation sensitive and evaporation insensitive species per biome. Bold horizontal lines indicate the median, with surrounding boxes representing the interquartile range (first quartile to third quartile). The whiskers indicate the range of values that are not outliers. Outliers (values of between 1.5 and 3 more than the interquartile range) are indicated by an open circle and extreme outliers (values more than 3 times the interquartile range away from the median) are indicated by a solid star.

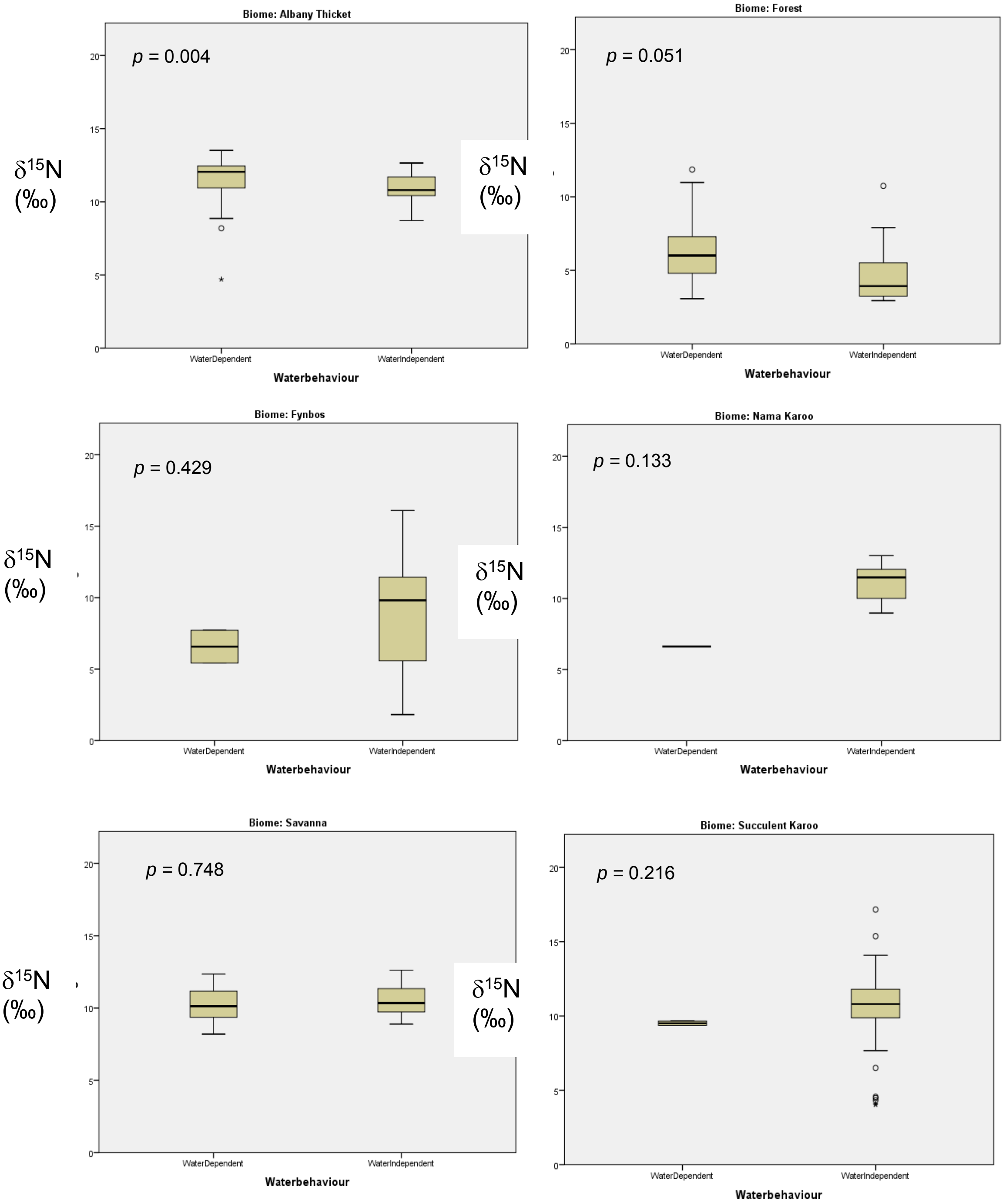

Figure 6. 11 Comparison of $\delta^{15}N_{collagen}$ (‰) for water dependent and water independent animals per biome. Bold horizontal lines indicate the median, with surrounding boxes representing the interquartile range (first quartile to third quartile). The whiskers indicate the range of values that are not outliers. Outliers (values of between 1.5 and 3 more than the interquartile range) are indicated by an open circle and extreme outliers (values more than 3 times the interquartile range away from the median) are indicated by a solid star.

In summary, there was no significant differences in $\delta^{15}N_{collagen}$ between ES and EI animals from the Albany Thicket, Savanna, Fynbos and Succulent Karoo biomes. The Forest biome had a higher median for EI animals, even though these animals are drought tolerant and are expected to have higher $\delta^{15}N_{collagen}$ values. Only in the Nama Karoo were EI animals more enriched in ^{15}N than ES. However since there were only two EI animals this is not a robust conclusion. The patterns for the WD/WI split were similar in that most biomes showed no significant differentiation between WD and WI. The Albany Thicket biome had a significant difference between WD and WI with the WD animals being more enriched in ^{15}N.

6.3.4 Results by biome

In the Forest biome, there were significant differences between $\delta^{15}N_{collagen}$ of browsers, grazers, carnivores and omnivores (Kruskal-Wallis H (3) = 23.62, $p < 0.001$). The median for browsers was 3.7‰ (n = 16) and for grazers was 8.8‰ (n = 4) (Figure 6.12a). These are significantly different ($p = 0.021$), although a larger sample size would increase confidence in these results. The median for omnivores was 5.9‰ (n = 45) and for carnivores was 8.2‰ (n=7). Values for carnivores were significantly different from browsers ($p < 0.001$) and omnivores ($p = 0.009$), the carnivores analysed here (bat-eared fox, caracal, genet, leopard, honey badger) do not consume these grazers (hippopotamus and buffalo) so trophic level differentiation was not necessarily expected. The difference between the median values for carnivores and browsers in this biome was 4.5‰, although this was not significant.

In the Fynbos biome (Figure 6.12b), there were significant differences between $\delta^{15}N_{collagen}$ of browsers, grazers, carnivores and omnivores (Kruskal-Wallis H (3) = 35.107, $p < 0.001$). Values for carnivores (median = 10.6‰) are significantly higher than omnivores (median 5.8‰, n = 97) ($p = 0.002$). The median for omnivores was significantly lower than grazers ($p < 0.001$). The median for browsers (5.9, n=16) was significantly lower than for grazers (p=0.029) and for carnivores (p=0.023).

In the Succulent Karoo biome (Figure 6.12c), there were significant differences between $\delta^{15}N_{collagen}$ of the omnivores and mixed feeders, grazers and browsers (Kruskal-Wallis H (4) = 32.541, $p < 0.001$). No trophic level differences could be determined due to a carnivore sample size of one. The median for browsers was 10.9‰ (n = 31) and that for grazers was 10.5‰ (n = 28). These were not significantly different ($p = 1.000$). The browsers in this biome had a large range of values (13.1‰).

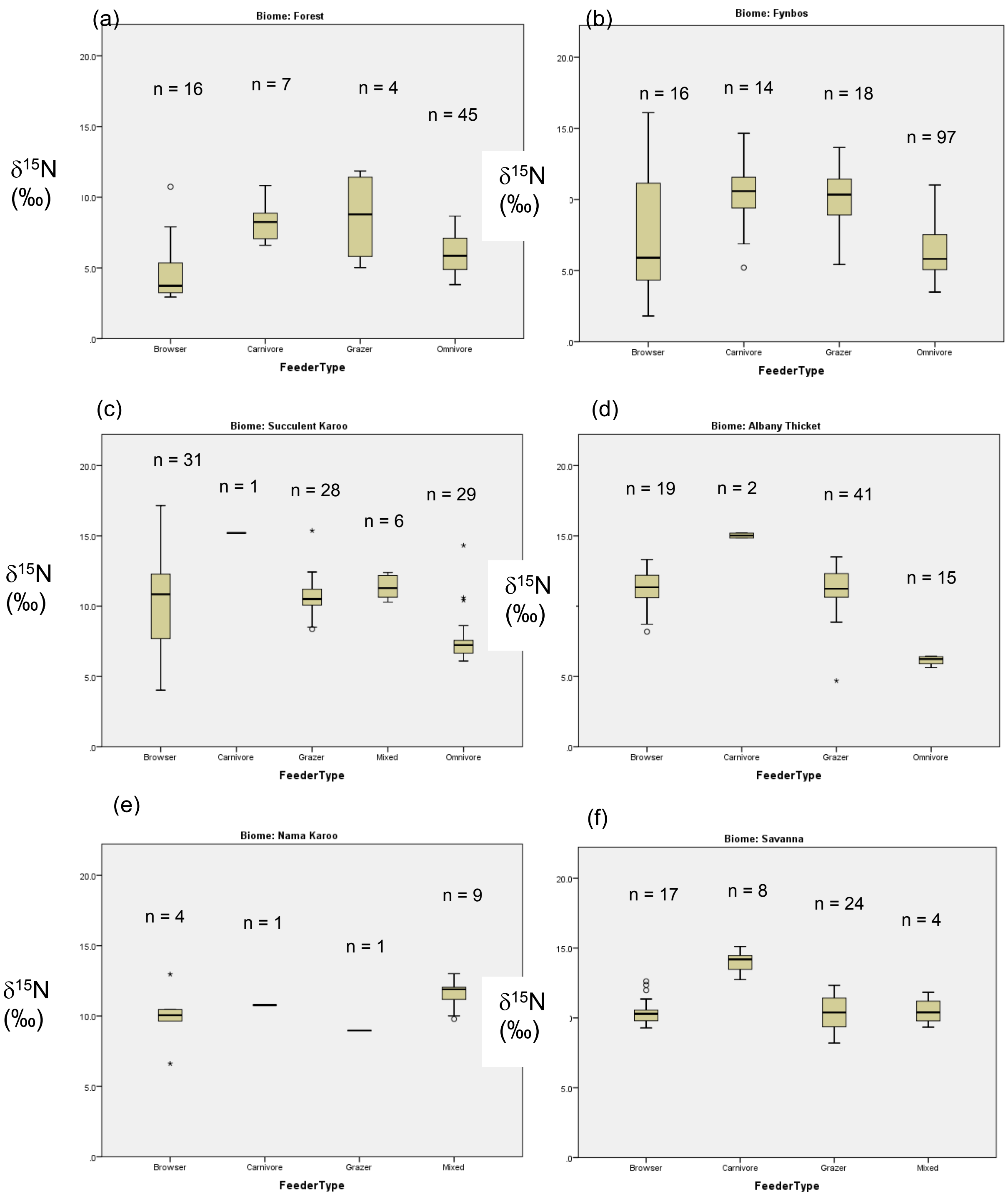

Figure 6. 12 $\delta^{15}N_{collagen}$ (‰) for the a) Forest, b) Fynbos, c), Succulent Karoo, d) Albany Thicket, e) Nama Karoo and f) Savanna biomes by feeder type. See legend to Fig. 6.5 for an explanation of the format of the plots.

In the Albany Thicket biome (Figure 6.12d), omnivores had significantly lower $\delta^{15}N_{collagen}$ than all other groups (carnivores, p = 0.004); browsers, p = 0.033; and grazers, p = 0.002) (Kruskal-Wallis H (3) = 18.80, p < 0.001). The $\delta^{15}N_{collagen}$ values for the highest trophic level (carnivores) were the most enriched (two samples – one lion and one spotted hyena). The next lowest trophic levels were 3.6‰ lower than the carnivore median for browsers and 3.8‰ lower for grazers.

In the Nama Karoo biome (Figure 6.12e), there was a significant difference between the mixed feeders (median = 11.9) and the browsers (median = 10.1) (Mann-Whitney Z = 2.47, p = 0.011). A larger sample size would increase confidence in this finding. Carnivore (10.8‰) and grazer (9.0‰) both only had one observation, so no analyses could be conducted with these groups.

In the Savanna biome (Figure 6.12f), the highest trophic level (carnivores) (median = 14.2‰, n = 8) had significantly higher $\delta^{15}N_{collagen}$ than browsers (median = 10.3‰, $p < 0.001$) and grazers (median = 10.4‰, $p < 0.001$) (Kruskal-Wallis H (3) = 20.12, $p < 0.001$). There were no significant differences between any of the other groups

The $\delta^{15}N_{collagen}$ values of grazers and browsers did not differ significantly in most biomes. There was a significant difference between browsers and grazers only in the Forest and the Fynbos biomes. Other than the Forest biome, carnivores had consistently higher $\delta^{15}N_{collagen}$ than the ungulates (browsers, grazers and mixed). Omnivores were only present in Succulent Karoo, Fynbos and Forest, and in two of these biomes were lower than the ungulates (Succulent Karoo and Fynbos). Omnivores had lower values than browsers and grazers in the Forest biome, but had higher values than omnivores.

6.3.5 Results by digestive physiology

Table 6.13 provides results by biome in terms of differences between ruminant[26] (foregut fermenters) and non-ruminant[27] (hindgut fermenters) ungulates. The number of hindgut fermenting ungulates in the sample was small, so caution is necessary when interpreting the results.

[26] Ruminants include: red hartebeest, springbok, blue duiker, blue wildebeest, bontebok, giraffe, hippopotamus, klipspringer, gemsbok, grey rhebuck, steenbok, grysbok, reedbuck, common duiker, buffalo, eland, bushbuck, and kudu.

[27] Non-ruminants include: black rhino, zebra, warthog, and bushpig.

Table 6. 13 $\delta^{15}N_{collagen}$ (‰) of non-ruminant (hindgut) and ruminant (foregut) ungulate species from all biomes. Non-ruminants were not sampled in the Savanna and Fynbos biomes (NA indicates a lack of samples).

	Non-ruminant				Ruminant			
Biome	N	Median	Minimum	Maximum	N	Median	Minimum	Maximum
Albany thicket	7	10.3	9.1	12.7	58	11.4	4.7	13.5
Forest	13	6.3	4.4	8.7	20	4.7	2.9	11.9
Fynbos	NA	NA	NA	NA	30	9.3	1.8	16.1
Nama Karoo	1	6.6	6.6	6.6	13	11.5	9	13
Savanna	NA	NA	NA	NA	45	10.3	8.2	12.6
Succulent Karoo	2	9.5	9.4	9.7	62	10.8	4	17.2

Albany Thicket and Forest biomes had adequate numbers of both ruminants and non-ruminants for making comparisons across environmental contexts. Mann-Whitney tests indicated that $\delta^{15}N_{collagen}$ values of ruminants compared with non-ruminants were not significantly different in the Albany Thicket ($Z = 0.94$, $p = 0.346$) whereas they were significantly different in the Forest biome ($Z = 6.367$, $p = 0.024$). In the Forest biome, $\delta^{15}N_{collagen}$ values are lower in ruminants than in non-ruminants.

6.3.6 Relationships between $\delta^{15}N_{collagen}$ and meteorological factors

In the following section, the relationships between $\delta^{15}N_{collagen}$ values and meteorological factors in the current study region were evaluated. This was done firstly by running correlations and secondly regression models to predict $\delta^{15}N_{collagen}$ based on the meteorological variables.

6.3.6.1 Correlations

The next section explores correlations between $\delta^{13}C_{collagen}$ and meteorological variables. The following table (6.14) provides results of the correlations (Spearman's rho) between $\delta^{13}C_{collagen}$ and all the meteorological factors.

Table 6. 14: Correlation coefficients for $\delta^{13}C_{collagen}$ and meteorological variables from all locations. The number of specimens varies across the rows because not all variables are available for all locations. 'Omnivore' includes ungulate omnivores and primate omnivores. Correlation coefficients are considered significant when p <0.05 (in bold). Mean annual precipitation (MAP), mean annual temperature (MAT), mean annual soil moisture stress (MASMS), mean annual potential evapotranspiration (MAPE), relative humidity (RH), summer aridity index (SAI), winter concentration of rainfall (WCR), moisture index (MI) and water deficit (WD).

Feeder type		MAP	MAT	MASMS	MAPE	RH	SAI	WCR	WD	MI
Browser	Correlation coefficient (r_s)	**-0.379****	0.108	0.190	**0.340****	-0.179	-0.168	**-0.413****	**0.342****	**-0.359****
	Sig. (2-tailed)	0.001	0.582	0.310	0.002	0.129	0.041	0.000	0.002	0.001
	N	102	102	86	102	102	102	102	102	102
Grazer	Correlation coefficient (r_s)	0.138	**0.590****	0.179	-0.131	0.177	**0.569****	**-0.564****	-0.131	0.138
	Sig. (2-tailed)	0.137	0.000	0.057	0.158	0.057	0.000	0.000	0.160	0.137
	N	117	117	113	117	117	117	117	117	117
Mixed	Correlation coefficient (r_s)	-0.036	0.370	0.415	0.369	**-0.462***	**0.462***	**-0.708****	0.205	-0.036
	Sig. (2-tailed)	0.885	0.119	0.077	0.119	0.047	0.047	0.001	0.399	0.885
	N	19	19	19	19	19	19	19	19	19
Omnivore	Correlation coefficient (r_s)	**-0.350****	-0.090	**0.568****	**0.412****	-0.154	0.083	**-0.485****	**0.439****	**-0.419****
	Sig. (2-tailed)	0.000	0.261	0.000	0.000	0.054	0.299	0.000	0.000	0.000
	N	158	158	134	158	158	158	158	158	158
Carnivore	Correlation coefficient (r_s)	**-0.550****	**0.683****	**0.765****	**0.527****	**-0.649****	0.328	**-0.746****	**0.530****	**-0.469****
	Sig. (2-tailed)	0.001	0.000	0.000	0.002	0.000	0.067	0.000	0.002	0.007
	N	32	32	26	32	32	32	32	32	32

**. Correlation is significant at the 0.01 level (2-tailed).

*. Correlation is significant at the 0.05 level (2-tailed).

As for $\delta^{13}C_{enamel}$, the $\delta^{13}C_{collagen}$ for carnivores is the dataset correlated with the largest number (eight out of nine) meteorological factors, with SAI the only exception. This pattern indicates that, as for $\delta^{13}C_{enamel}$, carnivores are an effective integrator of environmental influences on animal $\delta^{13}C$. $\delta^{13}C_{collagen}$ of grazers and mixed feeders are correlated with only three meteorological factors and browsers with five (See Table 6.14). While browsers show significant correlations with a five meteorological factors, the correlation coefficients are much lower than for carnivores, indicating more variance. It is interesting that the mixed feeders are correlated with three factors (RH, SAI and WCR), since in the $\delta^{13}C_{enamel}$ dataset they were not correlated with any meteorological factors.

Following these tests, regression models were run and are reported in the next section.

6.3.6.2 Simple regression

Univariate regressions were run for $\delta^{15}N_{collagen}$ against each individual meteorological factor. For ungulates, a summary of the outcome of each univariate regression is presented in Table

6.15. For ungulates, fixed variables included the feeder type (grazer, browser, mixed feeder or omnivore) and size of animal (small, medium, large, extra-large).

Table 6. 15: Summary outcome of regression models for $\delta^{15}N_{collagen}$ for ungulates against each meteorological factor individually. The adjusted r^2 is modified for the number of predictors in the model. For models with only one predictor, r^2 should suffice, but for consistency r^2 adjusted is reported. B is the unstandardised regression coefficient (the change in the isotope value with a one unit change in meteorological factor); t is the test statistic (used to test whether B is significantly different from zero). *p*-values that are significant at <0.05 are in bold. Mean annual precipitation (MAP), mean annual temperature (MAT), mean annual soil moisture stress (MASMS), mean annual potential evapotranspiration (MAPE), relative humidity (RH), summer aridity index (SAI), winter concentration of rainfall (WCR), moisture index (MI) and water deficit (WD).

Met.					95% Confidence interval			
variables	B	Std. error	t	*p*	Lower bound	Upper bound	r^2	r^2 adj
MAP	-0.005	0.001	-5.709	**< 0.001**	-0.006	-0.003	0.33	0.31
MAT	0.309	0.206	1.501	0.135	-0.097	0.715	0.24	0.22
MASMS	0.021	0.038	0.567	0.572	-0.053	0.096	0.09	0.07
MAPE	0.001	0.000	2.756	**0.006**	0.000	0.002	0.26	0.24
RH	-0.011	0.015	-0.723	0.470	-0.039	0.018	0.24	0.22
SAI	-0.003	0.002	-1.441	0.151	-0.008	0.001	0.24	0.22
WCR	-0.017	0.008	-2.196	**0.029**	-0.032	-0.002	0.25	0.23
WD	0.001	0.000	3.821	**< 0.001**	0.001	0.002	0.28	0.26
MI	-7.869	1.276	-6.167	**< 0.001**	-10.383	-5.356	0.34	0.32

MAP, MAPE, WCR, WD and MI were significantly correlated ($p<0.05$) with the $\delta^{15}N_{collagen}$, with r^2 values ranging between 0.14 and 0.30. MAT, MASMS, RH and SAI did not have significant correlations. Based on this data, the model predicts that for a change of 100 mm in MAP, the $\delta^{15}N_{collagen}$ value will decrease by 1.5‰. For a change of 1◦C in MAT, the isotope value will increase by 1.73‰. The r^2 values were much lower than in the previous data sets for $\delta^{13}C_{collagen}$, $\delta^{13}C_{enamel}$ and $\delta^{18}O$. Appendix 7 shows the outcome of the individual models for each meteorological factors.

For regression models using the carnivore subset (Table 6.16) all meteorological factors except SAI were significant and had much higher r^2 values than for ungulates. The r^2 of MAP and MI were the highest at 0.63 and 0.60 respectively.

The primate regression models (summary in Table 6.17) had extremely low r^2 values, even for those meteorological factors that were significant. This was a similar pattern to that seen for both $\delta^{13}C_{collagen}$ and $\delta^{13}C_{enamel}$. The highest r^2 was 0.26 for the correlation with MAPE, which was extremely low.

Table 6. 16: Summary outcome of the regression models for $\delta^{15}N_{collagen}$ for carnivores against each meteorological factor individually. The adjusted r^2 is modified for the number of predictors in the model. For models with only one predictor, r^2 should suffice, but for consistency r^2 adjusted is reported. B is the unstandardised regression coefficient (the change in the isotope value with a one unit change in meteorological factor); t is the test statistic (used to test whether B is significantly different from zero). *p*-values that are significant at <0.05 are in bold. Mean annual precipitation (MAP), mean annual temperature (MAT), mean annual soil moisture stress (MASMS), mean annual potential evapotranspiration (MAPE), relative humidity (RH), summer aridity index (SAI), winter concentration of rainfall (WCR), moisture index (MI) and water deficit (WD).

Met.					95% Confidence interval			
variables	B	Std. error	t	*p*	Lower bound	Upper bound	r^2	r^2 adj
MAP	-0.009	0.001	-7.387	**< 0.001**	-0.012	-0.007	0.65	0.63
MAT	1.580	0.350	4.507	**< 0.001**	0.864	2.295	0.40	0.38
MASMS	0.269	0.048	5.613	**< 0.001**	0.170	0.368	0.57	0.55
MAPE	0.004	0.001	5.485	**< 0.001**	0.003	0.006	0.50	0.48
RH	-0.131	0.034	-3.837	**0.001**	-0.201	-0.061	0.33	0.31
SAI	0.006	0.006	1.030	0.311	-0.006	0.017	0.03	0.00
WCR	-0.041	0.016	-2.634	**0.013**	-0.073	-0.009	0.19	0.16
WD	0.003	0.000	6.407	**< 0.001**	0.002	0.004	0.58	0.56
MI	-13.741	1.976	-6.953	**< 0.001**	-17.777	-9.705	0.62	0.60

Table 6. 17: Summary outcome of the regression models for $\delta^{15}N_{collagen}$ for primates against each meteorological factor individually. The adjusted r^2 is modified for the number of predictors in the model. For models with only one predictor, r^2 should suffice, but for consistency r^2 adjusted is reported. B is the unstandardised regression coefficient (the change in the isotope value with a one unit change in meteorological factor); t is the test statistic (used to test whether B is significantly different from zero). *p*-values that are significant at <0.05 are in bold. Mean annual precipitation (MAP), mean annual temperature (MAT), mean annual soil moisture stress (MASMS), mean annual potential evapotranspiration (MAPE), relative humidity (RH), summer aridity index (SAI), winter concentration of rainfall (WCR), moisture index (MI) and water deficit (WD).

					95% Confidence interval			
	B	Std. error	t	*p*	Lower bound	Upper bound	r^2	r^2 adj
MAP	-0.004	0.001	-4.955	**< 0.001**	-0.005	-0.002	0.15	0.14
MAT	-0.544	0.207	-2.623	**0.010**	-0.953	-0.134	0.05	0.04
MASMS	0.195	0.041	4.796	**< 0.001**	0.115	0.276	0.15	0.14
MAPE	0.004	0.001	7.188	**< 0.001**	0.003	0.005	0.27	0.26
RH	-0.099	0.018	-5.439	**< 0.001**	-0.136	-0.063	0.17	0.17
SAI	-0.007	0.002	-3.721	**< 0.001**	-0.010	-0.003	0.09	0.08
WCR	-0.010	0.008	-1.312	0.192	-0.025	0.005	0.01	0.01
WD	0.002	0.000	6.344	**< 0.001**	0.001	0.003	0.22	0.21
MI	-6.306	1.202	-5.245	**< 0.001**	-8.682	-3.929	0.16	0.16

6.3.6.3 'Best fit' regression model

Using the same methodology as in Chapter 5 for establishing a 'best model' (outlined in Section 4.5), the selection process led to MAPE and WCR being included in the model. The summary for ungulates is reported in Table 6.18. This regression was not significant and the adjusted r^2 was only 0.24. Thus the model did not explain the variability in the $\delta^{15}N_{collagen}$ values.

Table 6. 18: The output of the ungulate 'best fit' model using mean annual potential evapotranspiration (MAPE) and winter concentration of rainfall (WCR). r^2 = 0.262 (Adjusted r^2= 0.238).

Parameter	B	Std. error	t	*p*	95% Confidence interval	
					Lower bound	Upper bound
Intercept	6.326	1.678	3.771	< 0.001	3.021	9.630
[FeederType=Browser]	0.708	0.883	0.801	0.424	-1.032	2.447
[FeederType=Grazer]	1.829	0.877	2.085	0.038	0.101	3.556
[FeederType=Mixed]	3.871	0.961	4.027	< 0.001	1.977	5.764
[FeederType=Omnivore]	0^a					
[Size=Extra large]	-1.322	1.078	-1.227	0.221	-3.444	0.801
[Size=Large]	0.748	0.537	1.391	0.165	-0.311	1.806
[Size=Medium]	-1.108	0.703	-1.577	0.116	-2.492	0.276
[Size=Small]	0^a					
MAPE	0.001	0.001	1.815	0.071		0.002
WCR	-0.007	0.009	-0.762	0.447	-0.026	0.011

For the carnivore subset (summary in Table 6.19), MAPE and WCR were used again in the model. Although the r^2 value for the model is 0.466, only MAPE is significant, indicating that there is no benefit to be gained from combining MAPE with WCR. For primates (Table 6.20), the best fit model yielded a low r^2 value. Only MAPE is significant, indicating that there is no added value in combining MAPE with WCR.

Table 6. 19: The output of the carnivore 'best fit' model using mean annual potential evapotranspiration (MAPE) and winter concentration of rainfall (WCR). r^2 = 0.501 (Adjusted r^2= 0.466).

Parameter	B	Std. error	t	*p*	95% Confidence interval	
					Lower bound	Upper bound
Intercept	1.903	2.687	0.708	0.485	-3.593	7.399
MAPE	0.004	0.001	4.265	< 0.001	0.002	0.006
WCR	-0.001	0.016	-0.091	0.928	-0.033	0.030

Table 6. 20: The output of the primate 'best fit' model using mean annual potential evapotranspiration (MAPE) and winter concentration of rainfall (WCR). r2 = 0.267 (Adjusted r2= 0.256).

Parameter	B	Std. error	t	*p*	95% Confidence interval	
					Lower bound	Upper bound
Intercept	-1.760	1.306	-1.348	0.180	-4.343	0.822
MAPE	0.004	0.001	7.025	< 0.001	0.003	0.005
WCR	0.003	0.007	0.508	0.613	-0.010	0.017

6.3.6.4 Regression models by specific subsets

Individual species data were interrogated to see if a better model could be found. The species used for this analysis were red hartebeest and eland (Table 6.21).

Table 6. 21: r^2 values (r^2 adjusted in brackets) for the relationship between the $\delta^{15}N_{collagen}$ value and each of the meteorological factors for the two species (red hartebeest and eland) for which data is available at multiple sites. **. Correlation is significant at the 0.01 level (2-tailed). *. Correlation is significant at the 0.05 level (2-tailed).

	Red hartebeest (grazer)	Eland (browser)
MAP	0.07 (0.04)	0.39 (0.36)**
MAT	0.03 (0.00)	0.34 (0.32)**
MASMS	0.05 (0.02)	0.02 (-0.03)
MAPE	0.02 (-0.01)	0.28 (0.24)**
RH	0.03 (0.00)	0.13 (0.1)
SAI	0.00 (0.03)	0.04 (-0.00)
WCR	0.00 (-0.03)	0.38 (0.36)**
WD	0.03 (0.00)	0.32 (0.29)**
MI	0.07 (0.05)	0.42 (0.39)**

There were no significant correlations for the grazer (red hartebeest). The browsing species (eland) had moderate r^2 values for predicting $\delta^{15}N_{collagen}$ (MAP r^2 = 0.36; MAT r^2= 0.32; WCR r^2= 0.36 and MI r^2 = 0.39).

6.3.7 $\delta^{15}N_{collagen}$ summary

Although there were differences between browsers and grazers when all biomes are analysed together, at biome level this was only the case in the Forest and Fynbos biomes (all other biomes had similar values). In these two biomes, the grazers had significantly higher $\delta^{15}N_{collagen}$ values than browsers.

Browsers and primates showed significant but weak correlations between $\delta^{15}N_{collagen}$ and various meteorological factors. The grazers show almost no correlations. The $\delta^{15}N_{collagen}$ data suggests (much like the $\delta^{13}C_{collagen}$ and $\delta^{13}C_{enamel}$ data) that using complex regression models incorporating multiple meteorological factors does not add any value, since the r^2 values are similar for the combination models and for those based on individual meteorological factors.

6.4 Projecting into the past: using $\delta^{18}O$ to predict $\delta^{15}N_{collagen}$

To determine if $\delta^{18}O_{enamel}$ could be used to predict $\delta^{15}N_{collagen}$, correlations between $\delta^{15}N_{collagen}$ and $\delta^{18}O_{enamel}$ were plotted. In terms of feeding preference (Table 6.22), correlations for carnivores and omnivores were the highest, with r^2 values of 0.164 and 0.115 respectively. Browsers, while significant (p = 0.002) has a low r^2 value of 0.097.

Table 6. 22: Correlation coefficients for the faunal groups based on dietary preference: browsers, grazers, mixed feeders, carnivores, and omnivores. **Correlation is significant at the 0.01 level (2-tailed). *Correlation is significant at the 0.05 level (2-tailed).

FeederType		N	r	r^2
Browser	Correlation Coefficient		0.312**	0.097**
	Sig. (2-tailed)	94	0.002	0.002
Grazer	Correlation Coefficient		-0.022	0.048
	Sig. (2-tailed)	101	0.830	0.830
Mixed	Correlation Coefficient		0.342	0.117
	Sig. (2-tailed)	19	0.152	0.152
Carnivore	Correlation Coefficient	32	0.405*	0.164
	Sig. (2-tailed)		0.022	0.022
Omnivore	Correlation Coefficient	157	0.339**	0.115
	Sig. (2-tailed)		< 0.001	< 0.001

The only compelling correlation between N and O was revealed when ungulate species were interrogated according to ES/EI/WD/WI (Table 6.23). For these data, WD animals exhibited the strongest relationship between $\delta^{15}N_{collagen}$ and $\delta^{18}O_{enamel}$ (r^2 = 0.53, n = 62. (Figure 6.14). Of the ungulates, only browsers showed a significant correlation (r^2 = 0.097) (Table 6.20). Grazers and mixed feeders did not demonstrate significant relationships, although the sample size for mixed feeders was too small to allow any meaningful inferences. None of these r^2 values is sufficiently high to enable confident prediction of $\delta^{15}N_{collagen}$ from $\delta^{18}O_{enamel}$.

For ES and EI species, correlations between $\delta^{15}N_{collagen}$ and $\delta\ ^{18}O_{enamel}$ approached significance for both groups, but with low r^2 values (EI=0.07 and ES=0.10) (Table 6.23). WD animals exhibited the strongest relationship between $\delta^{15}N_{collagen}$ and $\delta^{18}O_{enamel}$ (r^2 = 0.53, n = 62). WI animals did not show a significant relationship (r^2 = 0.02, n = 165).

Table 6. 23: Correlation coefficients for the ungulate group, by a) evaporation sensitive (ES)/evaporation insensitive (EI) and b) water dependent (WD) and water independent (WI) categories. **. Correlation is significant at the 0.01 level (2-tailed).

(a)		r	r^2
Evaporation insensitive		0.270**	0.073**
	Sig. (2-tailed)	0.003	0.003
	N	115	115
Evaporation sensitive		0.318**	0.101**
	Sig. (2-tailed)	0.001	0.001
	N	112	112

(b)		r	r^2
Water independent		0.142	0.02
	Sig. (2-tailed)	0.069	0.069
	N	165	165
Water dependent		0.728**	0.530**
	Sig. (2-tailed)	0.000	0.000
	N	62	62

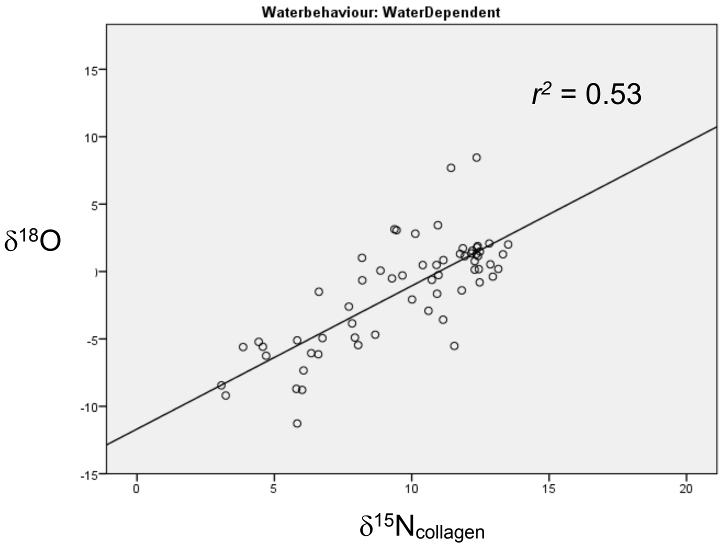

Figure 6. 13 Scatter plot for $\delta^{18}O_{enamel}$ (‰) against $\delta^{15}N_{collagen}$ (‰) for water dependent ungulates.

6.5 Comparing $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$

This section will describe intra-individual variation in $\delta^{13}C$ ratios in bone collagen and enamel. Where both $\delta^{13}C_{collagen}$ and $\delta^{13}C_{enamel}$ were available (Refer to Appendix 7), $\Delta_{enamel\text{-}collagen}$ was calculated. The data were non-normally distributed (Kolmogorov-Smirnov D (403) = 0.104, $p < 0.001$).

Figure 6.15 plots $\delta^{13}C_{collagen}$ against $\delta^{13}C_{enamel}$ for carnivores, primates and ungulates, showing the linear regressions for each group. $\delta^{13}C_{collagen}$ and $\delta^{13}C_{enamel}$ were strongly correlated for all of these groups: ungulates (r^2 = 0.77), primates (r^2 = 0.69) carnivores (r^2 = 0.66).

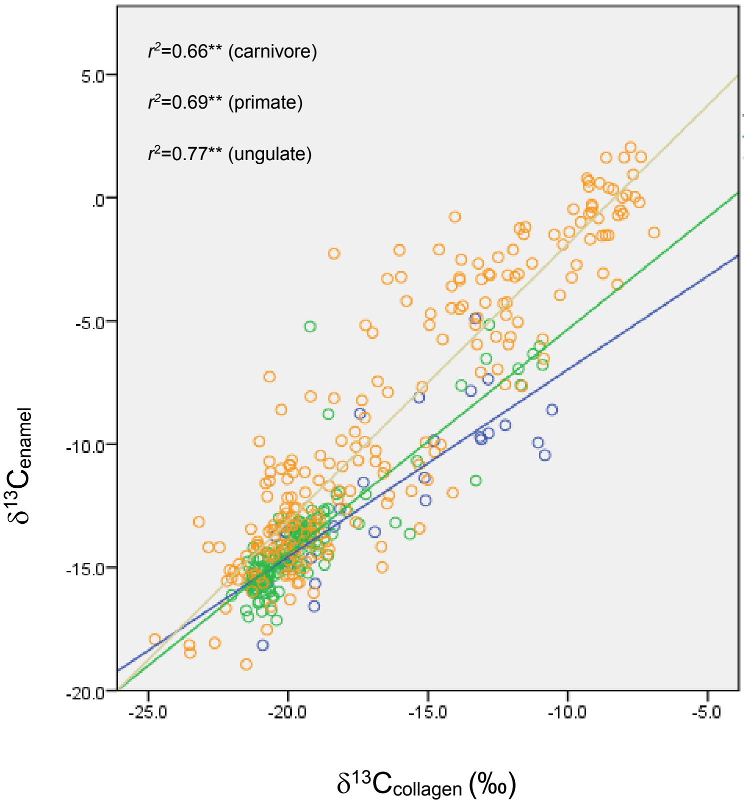

Figure 6. 14 Correlation between $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$ for carnivores (blue), primates (green) and ungulates (yellow). All relationships are significant (p<0.01).

Median $\Delta_{enamel\text{-}collagen}$ was largest for ungulates (7.1‰; mean = 7.3±2.3‰) compared with primates (5.5‰; mean = 5.5±1.2‰) and carnivores (5.0‰; mean = 4.6±1.9‰). This pattern is similar to that reported by Lee-Thorp *et al*. (1989): their mean $\Delta_{enamel\text{-}collagen}$ was 6.8 ± 1.4‰ for herbivores, 5.2 ± 0.1‰ for omnivores and 4.3 ± 1.0‰ for carnivores. A Kruskal-Wallis test revealed that the ungulates were significantly different to both the primates (p<0.000) and the carnivores (p<0.000). Primates and carnivores are not significantly different to each other (p=0.220).

For ungulates grouped by feeding preference, grazers had a higher $\Delta_{enamel\text{-}collagen}$ value (median = 8.6) than other ungulate subtypes and were significantly different from both browsers and omnivores (p < 0.001) (Kruskal-Wallis H (3) = 49.360, p < 0.001). Mixed feeding species had the next highest $\Delta_{enamel\text{-}collagen}$ value at 7.2, while the browsers and omnivorous ungulates were the lowest with medians of 6.2 and 6.0 respectively. The higher grazer value could be because in this data set the grazers are generally bigger animals (for example buffalo, red hartebeest, eland). For ungulates grouped by feeding preferences (Figure 6.49), the correlation between $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$ was low (browsers r^2 = 0.26, grazers r^2 = 0.61, mixed feeders r^2 = 0.22, omnivores r^2 = 0.03). These correlations were significant except in the case of the omnivore group.

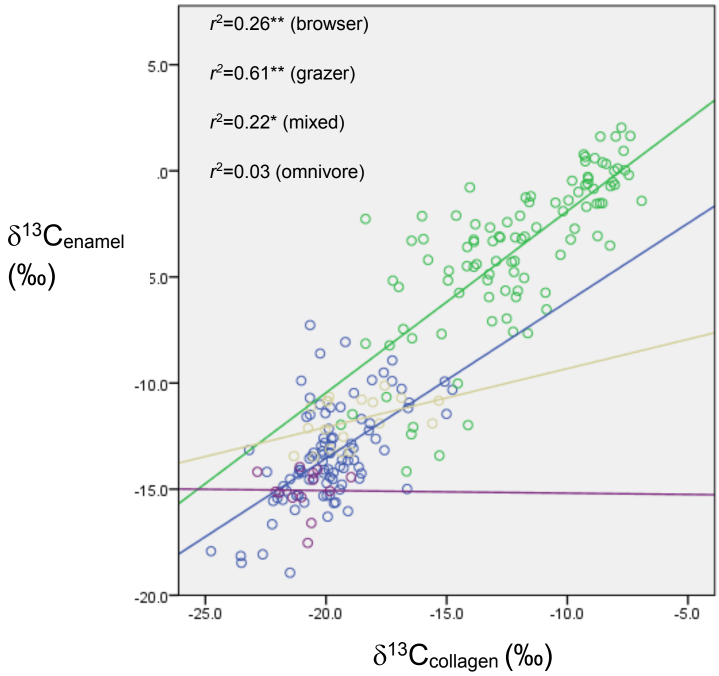

Figure 6. 15 Observed relationship between the $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$ of ungulates by feeding preference. Browsers (blue), grazers (green), mixed feeders (beige) and omnivores (purple). r^2 values with ** are significant at p<0.01, while r^2 values with * are significant at p <0.05).

Since the amount of methane (which is strongly depleted in ^{13}C when compared with source CO_2) produced in ruminants and non-ruminants differs, the data were analysed by splitting the ungulates according to the type of digestion (ruminant vs. non-ruminant). The median $\Delta_{enamel\text{-}collagen}$ value for ruminants was 7.2 (mean = 7.4 ± 2.3, n = 169) and for non-ruminants was 6.0 (mean = 6.0 ± 1.6, n = 23). Although both correlations were significant (Figure 6.17), ruminants had a higher r^2 value (r^2 = 0.76) than non-ruminants (r^2 = 0.61).

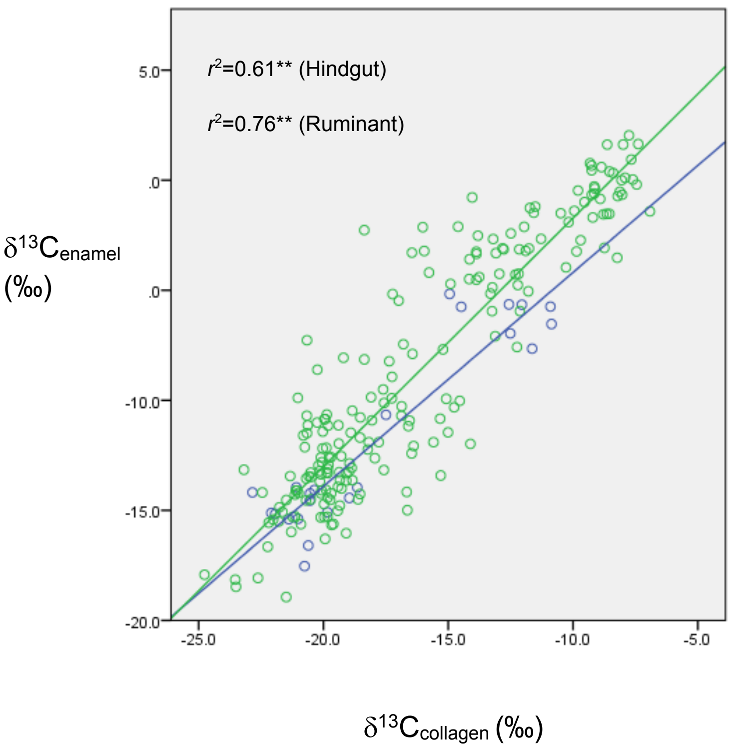

Figure 6. 16 Observed relationship between the $\delta^{13}C_{enamel}$ value and $\delta^{13}C_{collagen}$ of ungulates by type of fermenter. Ruminants (green) and Hindgut (blue). r^2 values with ** are significant at p<0.01, while r^2 values with * are significant at p <0.05).

As methane production could be influenced by size, the data were also analysed according to size (Figure 6.18). The medians per size category showed that the larger the animal, the larger the difference between $\delta^{13}C_{collagen}$ and $\delta^{13}C_{enamel}$ (Extra-large = 9.0; Large = 8.5; Medium =6.4; Small = 5.9) (Kruskal-Wallis H (3) = 55.206, p < 0.001). By excluding the two 'extra-large' animals, pairwise comparisons indicated that medium and small animals were similar to each other but differed significantly from large animals (p < 0.001). This could be because larger animals have slower metabolic rates or simply produce more methane. While all correlations were significant, the 'large' animals had the highest correlation (r^2 =0.78), which decreased with size.

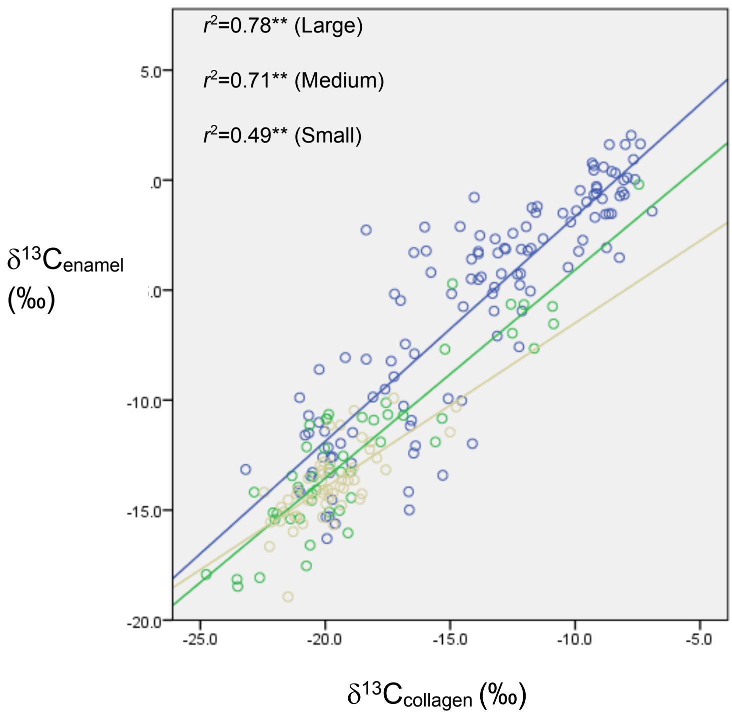

Figure 6. 17 Observed relationship between the $\delta^{13}C_{enamel}$ value and $\delta^{13}C_{collagen}$ of ungulates by size. Large (blue), Medium (green) and small (beige). r^2 values with ** are significant at p<0.01, while r^2 values with * are significant at *p* <0.05.

When ungulates were separated by evaporation sensitivity (Figure 6.19), EI species (those not eating tree leaves or shrubs) had a median of 8.4‰ (mean 8.1 ± 2.5‰, n = 115), while ES species had a median of 6.5‰ (mean = 6.6 ± 1.9‰, n = 112). These were significantly different (Mann-Whitney Z = 5.39, $p < 0.001$). Although both relationships are significant, EI ungulates had a much higher correlation (r^2 =0.72) than ES ungulates (r^2 =0.27).

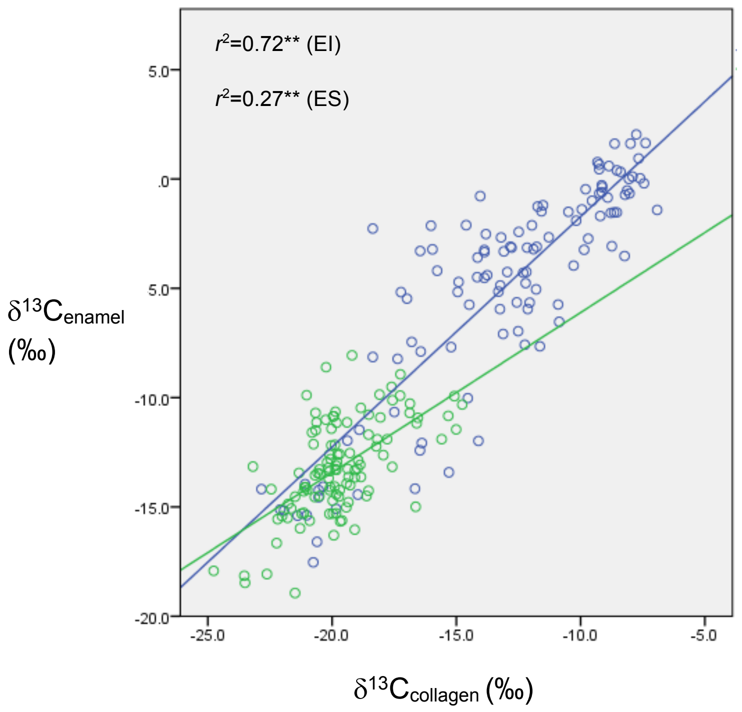

Figure 6. 18 Observed relationship between the $\delta^{13}C_{enamel}$ value and $\delta^{13}C_{collagen}$ of ungulates by evaporation sensitivity. EI (blue) and ES (green). r^2 values with ** are significant at p<0.01, while r^2 values with * are significant at <0.05.

Table 6.24 shows $\Delta_{enamel\text{-}collagen}$ per species for species with six or more individuals. The two suids (bushpig and warthog) had some of the smallest $\Delta_{enamel\text{-}collagen}$ values (mean 5.6‰ and mean 5.9‰, respectively). Other species with low values included small ungulates such as steenbok and grysbok (*Raphicerus* sp). *Tragelaphus* also had relatively low $\Delta_{enamel\text{-}collagen}$ values (bushbuck mean = 5.1‰ and kudu mean = 5.8‰). The highest $\Delta_{enamel\text{-}collagen}$ values found were for the grazer *Syncerus caffer* (mean = 9.5‰).

Table 6. 24: Summary of descriptive statistics of $\Delta_{enamel\text{-}collagen}$ of ungulates by species.

Species	N	Range	Minimum	Maximum	Median	Mean	Std. deviation
Raphicerus melanotis (grysbok)	6	1.7	5.3	7.0	6.4	6.3	0.7
Phacochoerus africanus (warthog)	7	2.9	4.0	6.9	5.6	5.6	1.2
Tragelaphus scriptus (bushbuck)	7	3.8	3.1	6.8	5.0	5.1	1.3
Raphicerus campestris (steenbok)	8	5.1	3.6	8.7	6.2	6.1	1.6
Raphicerus sp (grysbok/steenbok)	8	2.6	4.6	7.1	5.4	5.5	0.8
Tragelaphus strepsiceros (kudu)	9	5.6	1.6	7.2	6.6	5.8	1.7
Potamochoerus larvatus (bushpig)	13	5.4	3.2	8.7	6.0	5.9	1.5
Antidorcas marsupialis (springbok)	19	5.8	3.7	9.5	7.2	7.2	1.6
Syncerus caffer (buffalo)	21	6.9	6.3	13.3	9.4	9.5	1.9
Sylvicapra grimmia (common duiker)	24	4.4	4.0	8.4	5.9	6.0	1.2
Alcelaphus buselaphus (red hartebeest)	28	11.4	4.7	16.1	8.4	8.2	2.1

The $\Delta_{enamel-collagen}$ for this data set varied across biomes (Table 6.25). For carnivores, there were no significant differences across biomes (Kruskal-Wallis H (5) = 5.438, p = 0.365). For primates, there were significant differences (Kruskal-Wallis H (5) = 13.875, p = 0.003). Values from the Succulent Karoo were significantly different from the Forest (p = 0.005) and Fynbos biomes (p = 0.024). Ungulates also showed significant differences (Kruskal-Wallis (H (5) = 25.312, p < 0.001). The $\Delta_{enamel-collagen}$ in the Fynbos, Forest and Succulent Karoo were smaller than the overall median, while in the Albany Thicket, Nama Karoo and Savanna they were larger. Values for the Forest biome were significantly different from the Albany Thicket (p = 0.014). The Savanna biome displayed the biggest $\Delta_{enamel-collagen}$ value at 8.7, which was significantly larger than the Forest biome (p < 0.001) and the Succulent Karoo biome (p = 0.012). In all cases the Forest biome had a smaller difference than the overall median for that category.

Table 6. 25 Summary of $\Delta_{enamel-collagen}$ (mean and median) for carnivores, primates and ungulates by biome.

Animal type	Mean/median	Albany Thicket	Forest	Fynbos	Nama Karoo	Savanna	Succulent Karoo
Carnivore	Median	5.3	3.4	5.2	3.8	3.1	
	Mean	5.3	4.0	5.0	3.8	3.9	
Primate	Median	4.9	5.0	5.5			5.9
	Mean	5.4	5.0	5.4			6.1
Ungulate	Median	7.6	6.3	6.7	7.6	8.7	6.6
	Mean	7.6	6.0	6.4	7.6	8.3	7.0
Ungulate – Carnivore	Based on median	2.3	3.2	1.5	3.8	5.6	2.1
(or $\Delta\Delta$)	Based on mean	2.3	2.0	1.4	3.8	4.4	-1.7

In summary, for this data set the carnivores had the smallest $\Delta_{enamel-collagen}$, the ungulates had the largest $\Delta_{enamel-collagen}$, while primates fell in between these values. The values varied across biomes (Table 6.23), with the smallest $\Delta_{enamel-collagen}$ found mostly in the Forest biome. Within the subset ungulates, the differences in these values differed by body size, sensitivity to evaporation levels and type of digestion.

6.7 Bone collagen summary

Chapter 6 presented the $\delta^{13}C_{collagen}$ and $\delta^{15}N_{collagen}$ values as well as the intra-individual data ($\delta^{13}C_{enamel}$ vs $\delta^{13}C_{collagen}$). As with $\delta^{13}C_{enamel}$, the $\delta^{13}C_{collagen}$ values differed across biomes. Although browsers had more negative $\delta^{13}C$, some biomes were significantly different from others. The ranges of values for browsers were much smaller than seen in $\delta^{13}C_{enamel}$ of browsers. Grazers in the Fynbos biome were much more depleted in ^{13}C than other biomes. This was expected since this is a predominantly winter rainfall biome. Primate $\delta^{13}C_{collagen}$ was poorly correlated with all meteoroligical factors. The $\delta^{15}N_{collagen}$ values for browsers and grazers were not significantly different in most biomes, but values for carnivores were consistently more positive than those for other groups. In most of the data sets ($\delta^{13}C_{collagen}$, $\delta^{13}C_{enamel}$, $\delta^{18}O_{enamel}$ and $\delta^{15}N_{collagen}$) values in the Forest biome were most negative. The relationships between $\delta^{13}C_{collagen}$ and meteorological factors were high for ungulates and most strongly correlated with MAT (r^2 = 0.60), MASMS (r^2 = 0.52), SAI (r^2 = 0.63) and WCR (r^2 = 0.65). The latter two correlations could be more robust once a longer period of meteorological data is added. For $\delta^{15}N_{collagen}$ the relationships were weaker for ungulates (the r^2 values were ≤ 0.32). Carnivore $\delta^{15}N_{collagen}$ had significant correlations (at $p<0.05$) with the highest r^2 values. Primate $\delta^{13}C_{collagen}$ and $\delta^{15}N_{collagen}$ was again not well correlated with any meteorological factors, as was found to be the case for enamel carbonate.

Chapter 7: Discussion and conclusion

The goal of this thesis was to establish the variability in $\delta^{13}C$, $\delta^{15}N$ and $\delta^{18}O$ of wild fauna across the environmental gradient of the winter rainfall area of South Africa, including adjacent regions for comparative purposes. This study aimed to explore the nature and extent of possible correlations between environmental variables and $\delta^{13}C$, $\delta^{15}N$ and $\delta^{18}O$ in faunal bone collagen and tooth enamel, since these are the tissues most commonly analysed in archaeological and palaeontological studies.

The first section of this chapter focusses on the variation across environmental gradients, looking firstly at $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$, secondly at $\delta^{18}O_{enamel}$ and finally at $\delta^{15}N_{collagen}$. The second section focuses on the relationship between isotope measurements of different tissues within one individual. The final section discusses how the modern baseline generated in this study can assist in the interpretation of variations observed in isotopic signals of faunal assemblages from archaeological and palaeontological sites.

7.1 Isotopic variation across the environmental gradient

7.1.1 $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$

Since the focus of this project was the C_3 winter rainfall area, the expectation was that both grazers and browsers would reflect prominently C_3 diets. However, the consumption of C_4 grass was greater than expected, even in the Fynbos and Succulent Karoo biomes, which receive the highest proportions of winter rainfall and have the fewest species of C_4 grasses (Vogel *et al.*, 1978).

There were 14 grazers from the Fynbos Biome that yielded $\delta^{13}C_{collagen}$ values; 11 were from the West Coast National Park, and three were from the De Hoop Nature Reserve and Bontebok National Park. The sample was small partly because most of the large, mammalian fauna has been eradicated from this region but also because grazers (other than bontebok and red hartebeest) have not been abundant in the Fynbos for at least the last 10 000 years (Skead, 1980; Klein, 1983; Hendey, 1983; Faith and Behrensmeyer, 2013), presumably due to the availability of only limited quantities of grass. De Hoop and Bontebok National Park, though part of the Fynbos biome, have large areas of Coastal Renosterveld vegetation which include 5-25% C_4 grass species (Vogel *et al.,* 1978). The pattern of enrichment (values of up to -5‰ for $\delta^{13}C_{enamel}$ and up to -13‰ for $\delta^{13}C_{collagen}$) in animals from these areas indicates that they were seeking out areas of C_4 grasses and feeding on them preferentially. $\delta^{13}C_{collagen}$ values from the West Coast National Park were not as positive (median -18.3‰, with least negative value -17.9‰) because the grasses in this part of the Fynbos Biome are mostly C_3 species (Vogel *et al.,* 1978).

This observation of selective feeding behaviour is consistent with the results of other studies of grazers in this region. Radloff (2008) reported similar $\delta^{13}C_{collagen}$ for bontebok and red hartebeest, as well as other grazers from De Hoop and Bontebok National Park. He calculated that the animals' dependence on C_4 grass ranged from 23% to 78%. Midgley and White (2016) found the average $\delta^{13}C$ value of bontebok dung from De Hoop to be -20.1 ± 2.4‰. This reflects approximately equal consumption of C_3 and C_4 grasses. It should be noted that these dung samples were collected over a period of only a few days and therefore do not reflect seasonal dietary shifts. Although dung $\delta^{13}C$ values have been shown to be broadly consistent with diet, they have also shown to over-represent more fibrous and therefore less digestible components of diet (Codron *et al.,* 2011). In archaeological datasets, Sealy *et al.* (2016) report $\delta^{13}C_{enamel}$ values of -1.1 to -5.6‰ for the grazer *Redunca fulvorufula* from Boomplaas Cave, situated in the Succulent Karoo biome. These values are significantly less negative than those of other grazers from the same site, indicating that *Redunca fulvorufula* were grazing selectively on C_4 grass. Although this has previously not been well-documented in isotopic studies, species-specific dietary preferences expressed in the $\delta^{13}C$ values of grazers are expected. Thus, one should be sensitive to this potential problem when lumping grazers together.

In three out of the four animal groups sampled from the Forest biome, the $\delta^{13}C$ values were the most negative of all the biomes studied. The area receives rain year round and contain C_3 and C_4 grasses. The four grazing animals (three hippopotami and one buffalo, all historic specimens) from this biome show substantial variation in $\delta^{13}C_{collagen}$, with values of -9.7‰, -11.8‰ and -16.6‰ for the hippopotami and -9.7‰ for the buffalo. Three buffalo excavated from the archaeological site of Nelson Bay Cave, dating within the last 2000 years, had $\delta^{13}C_{collagen}$ values almost as high (-12.3‰, -11.1‰ and -10.9‰) (Sealy, 1996), indicating that there was a substantial amount of C_4 grass in the area in the past and/or that the grazers sought it out. Vegetation near Nelson Bay Cave today consists of a mosaic of forest, scrub and more open areas where grasses are a common element (Mucina and Rutherford, 2006). Hippopotami graze mainly near rivers and marshes. Higher values for hippopotami have been reported in East Africa (Cerling *et al.*, 2008); that study analysed tooth enamel and found mean $\delta^{13}C_{enamel}$ of -3.6‰, which would correspond to $\delta^{13}C_{collagen}$ of about -12.6‰. These authors reported a large range of $\delta^{13}C$ values for hippopotami and inferred that their diets were quite variable.

Given the biases introduced by selective feeding in grazers, browsers as a group are likely to be more useful environmental proxies. While browsers consumed overwhelmingly C_3 diets, their $\delta^{13}C_{collagen}$ values varied with the most negative values occurring in the Forest and Fynbos biomes and the least negative in the Albany Thicket, Nama Karoo and Succulent Karoo. These differences can be attributed to differences in the vegetation of the regions. In the Forest biome, $\delta^{13}C$ values for C_3 photosynthesisers are expected to be relatively negative due to high rainfall and moderate temperatures (Kohn, 2010; Diefendorf *et al.*, 2010). Additionally, plants in dense areas of forest are more likely to experience the canopy effect (van der Merwe and Medina, 1991; Cerling *et al.*, 2004). These factors could possibly result in the most negative $\delta^{13}C$ values for browsers in the Forest biome compared to all other biomes in this study.

At the other end of the range, browsers from the Albany Thicket, Nama Karoo and Succulent Karoo show the least negative $\delta^{13}C$ values due to more arid conditions and/or the inclusion of succulents in their diets. In the Albany Thicket, the favoured food plant spekboom (*Portulacaria afra)* is able to use CAM photosynthesis and is very likely to be an important driver of less negative browser $\delta^{13}C$. The Succulent Karoo, as its name implies, is home to a wide variety of succulent plants, many of which are CAM photosynthesizers. For the purposes of this thesis, it is not important whether the less negative browser $\delta^{13}C$ in these biomes results from the consumption of C_4 grasses, succulents, or changes in $\delta^{13}C_{foliar}$ values. The key point is that browsers are effective monitors of environmental and climatic conditions; grazer $\delta^{13}C_{enamel}$ is significantly correlated with only three meteorological factors while browser $\delta^{13}C_{enamel}$ is significantly correlated with seven (Table 5.4 in Results). The same pattern is seen in $\delta^{13}C_{collagen}$, with three and five meteorological factors respectively (Table 6.2).

Biomes with greater proportions of summer rainfall showed larger differences between grazers and browsers than the more strongly winter rainfall biomes. For example, $\delta^{13}C_{collagen}$ of grazers and browsers from the Fynbos Biome were not significantly different (Table 7.1). $\delta^{13}C_{enamel}$ of grazers and browsers in this biome were significantly different, though the sample size would need to be larger (grazer enamel: n=3) to increase confidence in this result. In the other biomes, browsers and grazers were significantly different from each other (Table 7.1). This is expected since most of these biomes (other than the Succulent Karoo) have some summer rainfall where some C_4 grass would be present. The similarity between browsers and grazers in ancient settings has also been noted. $\delta^{13}C_{enamel}$ values for browsers (n=20) from Elandsfontein (dated to between 600kya and 1mya) ranged between -11.1‰ and -14.8‰ while grazers (n=62) were between -7.5‰ and -12‰ (Luyt *et al.*, 2000; Lehmann *et al.*, 2016). At Hoedjiespunt (dated to between 40 kya and 240 kya) $\delta^{13}C_{enamel}$ values for browsers (n=10) were -8‰ to -11‰ and grazers (n=20) were between -6‰ and -12‰ (Hare and Sealy, 2013). Neither of these pairs of values were significantly different.

Table 7. 1 Differences in $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$ for grazers and browsers across biomes. (The Succulent Karoo biome was excluded from further discussion because a comparison cannot be made, due to the two different groups of gemsbok from the Anysberg Nature Reserve reported in Results Chapters 5 and 6).

	$\delta^{13}C_{enamel}$		**$\delta^{13}C_{collagen}$**	
Biome	**Significant difference between grazers and browsers**	***p***	**Significant difference between grazers and browsers**	***p***
Forest	No grazers	-	Yes	<0.001
Fynbos	Yes (*p*=0.001)	0.001	No	0.094
Succulent Karoo	Yes (*p*<0.001)	<0.001	Yes	<0.001
Nama Karoo	N/A (not enough grazers)	-	N/A (not enough grazers)	-
Savanna	Yes (p<0.001)	<0.001	Yes	<0.001
Albany thicket	Yes (p<0.001)	<0.001	Yes	<0.001

Of all the animal groups, mixed feeders were the least helpful as environmental proxies. The contemporary mixed feeders displayed values towards the C_3 end of the spectrum, indicating that they were mostly browsing in all three biomes from which mixed feeders were available. The ranges of $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$ were small (values between -9.5 and -13.5‰ excluding outliers[28]), indicating that the animals were eating similar diets. Given the dietary flexibility that mixed feeders may exercise when required, they may not be a good choice for use as environmental proxies.

The $\delta^{13}C_{enamel}$ in ungulates as a whole (with feeder type, body size as fixed variables) presented the strongest relationship with meteorological factors of all animals tested, with MAT and SAI having an r^2 value of 0.75 ($p < 0.001$) while the r^2 value for WCR was 0.74 ($p = 0.015$). In this dataset, the relationship between ungulate $\delta^{13}C_{enamel}$ and MAP was not significant ($p = 0.277$). This is an important result because it is unexpected, based on previous research which established a strong correlation between MAP and plant $\delta^{13}C$ (Stewart *et al.*, 1995; Diefendorf *et al.*, 2010). The Diefendorf *et al.* (2010) dataset had an r^2 value of 0.55 for the relationship between leaf enrichment ($\Delta^{13}C$) and MAP. They analysed data from across the globe and there was a fair amount of variation per biome. Stewart *et al*. (1995) also found a relationship between MAP and $\delta^{13}C_{foliar}$. The $\delta^{13}C_{foliar}$ values decreased by 0.33‰ per 100 mm decrease in precipitation. However the current study indicates that variables other than MAP may better explain variations in animal $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$ compositions. The generally low correlations with MAP echo the results from a field study in the Kruger National Park which

[28] Values more than 1.5 times the interquartile range away from the median

found only a weak relationship between $\delta^{13}C_{plant}$ and precipitation (Codron *et al.*, 2013). As the MAP range in the Kruger study was only 300-700 mm, this may not be broad enough for the relationship to be apparent (D. Codron, 2016, pers. comm.). The ungulate faunal data from this study suggest that $\delta^{13}C_{enamel}$ values decrease by 0.9$^{0}/_{00}$ for every 1°C that the average temperature decreases. A significant positive correlation between $\delta^{13}C_{enamel}$ and MAT implies increased availability of C_4/CAM foods for grazing ungulates in localities with a warmer growing season. When the category "ungulates" was narrowed to a single species (eland), the correlation was very poor for both $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$ (r^2 ranging between 0.13 and 0.24 for the significant correlations).The feeding preference classification of the eland is complicated. Some classify it as a mixed feeder (Gagnon and Chew, 2000; Skinner and Chimimba, 2005) although most classify it as a browser (Watson and Owen-Smith, 2000; Sponheimer *et al.,* 2000; Codron *et al.,* 2007; Wallington *et al.,* 2007). Radloff (2008) found that it can consume up to 25% C_4 grass in certain areas. Thus it should be considered that the eland $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$ could be driven by dietary preference.

Both $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$ had a strong relationship with the seasonality of rainfall variables. For a reduction of 10% in WCR, $\delta^{13}C_{enamel}$ increased by 0.23‰. SAI, the sum of precipitation between December and March, was another variable strongly correlated with $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$ for the ungulate group and also the species-specific group, the red hartebeest. As it increased, so did the $\delta^{13}C_{collagen}$ value. This trend has also been observed in the literature. Diefendorf *et al.* (2010) suggest that it may be the amount of rainfall that falls in the growing season, rather than the cruder MAP metric, that has a stronger relationship with $\delta^{13}C_{leaf}$. Murphy *et al.* (2007b) found that seasonal water availability alone explained around 68% of the variation in both $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$ in Australian kangaroos. When the kangaroos were separated into species, this increased to 78% for $\delta^{13}C_{collagen}$ and 77% for $\delta^{13}C_{enamel}$ (Murphy *et al.*, 2007b). Thus, these data support the hypothesis that seasonality of rainfall metrics have the strongest relationships with $\delta^{13}C$. More analysis is needed using a longer timespan of meteorological data to firm up this conclusion.

Carnivore $\delta^{13}C_{collagen}$ and $\delta^{13}C_{enamel}$ were significantly correlated with all nine meteorological factors, but the r^2 values were lower than for ungulates; r^2 for $\delta^{13}C_{collagen}$ ranged from 0.24 to 0.68 and r^2 for $\delta^{13}C_{enamel}$ ranged from 0.13 to 0.68. These results show that across a diverse set of biomes, although carnivores reflect MASMS well (r^2=0.68), this is not the case for ungulate $\delta^{13}C$ (not significant; p=0.187). MASMS is a good indicator of water availability for plant up-take. The strong relationship with carnivore $\delta^{13}C$ is interesting, since carnivores don't eat plants. Nevertheless, others have observed similarly close relationship between carnivore

$\delta^{13}C$ and climatic variables. Bump *et al.* (2007) measured the $\delta^{13}C$ of global atmospheric CO_2 over time and compared it with that of trees, large herbivore bone collagen and wolf bone collagen. $\delta^{13}C_{collagen}$ of wolves tracked the variation in global CO_2 most closely; the r^2 value was 0.64 compared with only 0.33 for herbivores and 0.12 for trees.

The most notable difference between the $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$ datasets is the markedly smaller ranges (excluding outliers) of $\delta^{13}C_{collagen}$ compared with $\delta^{13}C_{enamel}$ of browsers when the data is separated by biome (Table 7.2). This trend was true of all biomes except the Forest and Succulent Karoo. The most likely explanation for this difference is that teeth form over a relatively short period of time, while bone collagen represents a longer interval that better matches the annual-scale meteorological data used in this thesis. In other words, the short-term temporal fluctuations in diet are not smoothed out in enamel to the same extent as in bone collagen. The implication is that palaeo studies based on the tooth enamel of browsers may yield more variable results than those based on bone collagen. This is explored in the next section (intra-individual variation). Grazers, mixed feeders, carnivores and omnivores did not show a greater range in $\delta^{13}C_{enamel}$ compared with $\delta^{13}C_{collagen}$. Presumably, this means that in the winter rainfall region, these animals experience less seasonal variation in their diets than browsers. If the smaller ranges in collagen values are due to the fact that collagen represents a longer period of time than enamel, then it makes sense that the ranges are large in areas where there is more C_4 present (for example Albany thicket and Savanna). However, this does not explain why the $\delta^{13}C_{enamel}$ range is largest in the Fynbos biome.

Table 7. 2 Summary of the ranges for $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$ for browsers across biomes.

	$\delta^{13}C_{enamel}$		$\delta^{13}C_{collagen}$	
Biome	**Number**	**Range (‰)**	**Number**	**Range (‰)**
Forest	11	5.1	4	5.1
Fynbos	26	10.1	14	2.8
Succulent Karoo	34	5.3	27	8.4
Nama Karoo	7	6.1	1	3.0
Savanna	21	9.0	24	2.1
Albany Thicket	22	10.0	47	7.6

$\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$ of primates were poorly correlated with meteorological factors. It should be noted that the primates were collected from only four biomes, one being the Albany Thicket. To what extent the more positive Albany thicket values are driving this poor relationship is unknown. However, since primates are known to vary their diets according to their environments, they are unlikely to be useful environmental indicators except in the very broadest sense.

7.1.2 $\delta^{18}O_{enamel}$

The patterns in oxygen isotopes largely followed those observed in previous studies. Within an ecosystem (or locality), differences in $\delta^{18}O$ in animals are usually derived from reliance on different sources of water or from physiological differences between species. Some animals, such as grazers, drink surface water and are thus expected to be depleted in ^{18}O; others such as browsers, obtain their water from evaporatively enriched leaves and are enriched in ^{18}O (Levin *et al.,* 2006). Thus fauna from a given location can provide information on different aspects of the same environment.

The researchers Lee-Thorp and Sponheimer (Lee-Thorp and Sponheimer, 2010, Lee-Thorp and Sponheimer, 2005; Sponheimer and Lee-Thorp, 2001, Lee-Thorp, 2008) have found carnivores to be depleted in ^{18}O when compared with other animals from the same locality. This was the case in most of the biomes sampled in this study (Figure 7.3). In the Forest, Fynbos, Nama Karoo and Savanna biomes, carnivores had low $\delta^{18}O$ values while browsers had higher values. It is not fully understood why carnivores have low $\delta^{18}O$. It could be due to a reliance on drinking water or due to animal proteins being relatively depleted in ^{18}O (Yakir, 1992; Tredget *et al*., 1993; Sponheimer and Lee-Thorp, 2001, Kohn, 1996). Suggestions have also been made that liquid water that carnivores obtain from prey is less enriched in ^{18}O than free water in most herbivore plant foods (Lee-Thorp and Sponheimer, 2010). More research is required to test these hypotheses.

Table 7. 3 Summary of the most ^{18}O enriched and most depleted animal groups per biome.

Biome	Most depleted in ^{18}O	Most enriched in ^{18}O
Forest	Carnivores	Browsers
Fynbos	Carnivores	Browsers
Succulent Karoo	Omnivores	Mixed feeders
Nama Karoo	Carnivores	Browsers
Savanna	Carnivores	Browsers
Albany Thicket	No significant difference	

In the Succulent Karoo, mixed feeders displayed the highest $\delta^{18}O$ values and were significantly higher than the omnivores and grazers. Since mixed feeders were mainly browsing (C_3, negative $\delta^{13}C$ values), this finding fits with the animals that consume evaporatively enriched leaves. Levin *et al.* (2006) also found browsers such as giraffes and oryx (*Oryx beisa*) to have high $\delta^{18}O$ values compared to other animals consuming source water. This was also found in Lee-Thorp and Sponheimer (2003) and Lehmann *et al.* (2016). These findings led to the development of the aridity index.

The literature shows browsers to be enriched in ^{18}O relative to grazers (Kohn *et al.*, 1996; Sponheimer and Lee-Thorp, 1999). While there is one study that reported grazers to be more enriched in ^{18}O than browsers (Bocherens *et al*., 1996), it included only a single species of browser (black rhinoceros), which is an obligate drinker (Skinner and Chimimba 2006). In the current study, the $\delta^{18}O$ values of browsers and grazers were significantly different from each other only in the Fynbos biome (Table 7.4). In the Succulent Karoo, there is a significant difference between grazers and mixed feeders ($p = 0.040$), which are in effect browsers as discussed above. With the low numbers of samples in the Nama Karoo, it was difficult to draw any conclusions. The Savanna has a good sample size of both browsers (n=21) and grazers (n=33), which increases confidence in the outcome. More research is needed to resolve why there is no difference in this biome.

Table 7. 4 Summary of the *p*-values of grazers vs. browsers comparisons, following a Wilcoxon signed-rank test comparing all animal group $\delta^{18}O$ medians (a Kruskal-Wallis post-hoc test).

Biome	Grazers vs. browsers	Significance
Forest	no grazers	
Fynbos	Significantly different	$p < 0.020$
Succulent Karoo	Not significantly different	$p = 1.000$
Nama Karoo	Not significantly different	$p = 0.062$
Savanna	Not significantly different	$p = 0.764$
Albany Thicket	Not significantly different	$p = 0.058$

The Albany Thicket biome showed no significant differences in $\delta^{18}O$ across all animal groups (Tables 7.3 and 7.4). Many of the browsers were bushbuck and kudu. Kudu need to drink daily, which is not the “usual” behaviour for most other browsers (Skinner and Chimimba 2006). The Albany Thicket bushbuck have relatively negative $\delta^{18}O$ values, perhaps because bushbuck, like waterbuck, are known to sweat more than pant (Sponheimer and Lee-Thorp, 2001). Since sweating (loss of liquid water from the body) leads to lower $\delta^{18}O$ values in animal tissues than panting (loss of water vapour from the body), this may explain why bushbuck have lower $\delta^{18}O$ when compared with other animals. This may in part explain why the difference between browsers and grazers (or indeed ES and EI animals) is less than expected.

Albany Thicket has a high RH (80%), which may reduce differentiation of $\delta^{18}O$ according to mode of water intake and animal physiology.

Comparison of browsers across biomes shows that the most positive values occur in the Savanna biome while the most negative values occur in the Forest biome. Samples collected from the Forest biome came from close to the coast, whereas those from the Savanna biome came from much further inland. Given that the continental effect (described in Chapter 2) leads to increasingly positive $\delta^{18}O$ in precipitation with distance from the source of rain, these more positive values in Savanna are consistent with previously established research (McGuire and McDonnell, 2007; van der Merwe, 2013). The patterns can be explained by both gradients in $\delta^{18}O$ of meteoric water and local environmental effects within each biome.

Mixed feeders had relatively positive $\delta^{18}O_{enamel}$ values, with only a small range of variation. This group consisted of only one species, the arid-adapted springbok (*Antidorcas marsupialis*). Dietary studies (summarized in Skinner and Chimimba, 2005) show that springbok mostly browse evaporatively enriched leaves in the arid environments in which they live, grazing only when there is fresh, new grass after rain. It is therefore not surprising that positive $\delta^{18}O_{enamel}$ values (values which cluster with browsers) were noted in the Nama Karoo and Succulent Karoo biomes. Relatively positive $\delta^{18}O$ values for *Antidorcas marsupialis* (clustering with browsers rather than grazers) have also been measured at Equus Cave by Sponheimer and Lee-Thorp (1999a).

All four animal groups (browsers, omnivorous ungulates, carnivores and primates) were most depleted in ^{18}O in the Forest biome compared with other biomes. The Forest biome is a cool, moist environment with the highest RH of all the biomes studied, and thus evaporative enrichment of ^{18}O in leaves is less. In the Ituri forest, Cerling *et al.* (2004) found that most of the animals sampled had low $\delta^{18}O$ values. Only two colobus monkeys were more positive than other animals, perhaps due to their reliance on evaporatively enriched leaves high in the canopy. In the animals from the Forest biome in this study, not only were $\delta^{18}O_{enamel}$ values low, but $\delta^{13}C_{collagen}$ and $\delta^{13}C_{enamel}$ were also low. It can be inferred that the low $\delta^{13}C$ values are therefore driven mainly by moisture, rather than ^{13}C depleted CO_2 due to the canopy effect, since the canopy effect does not influence $\delta^{18}O$ (refer to Chapter 2, page 24).

There were significant differences in $\delta^{18}O$ between ES and EI animals (Table 7.5) with the expected pattern of more ^{18}O enrichment in ES animals noted in the Fynbos, Succulent Karoo, Nama Karoo and Albany thicket biomes. Lehmann *et al*. (2016), Levin *et al*. (2006) and Lee-Thorp (2008) all found that animals that consume evaporatively enriched leaves have more positive $\delta^{18}O$ values. Hotter biomes (Savanna and Nama Karoo) were more enriched in ^{18}O

for both ES and EI groups. The Albany thicket displayed less positive values than Savanna and Nama Karoo, likely due to slightly higher rainfall in this biome. Only the Forest biome showed no significant difference between the EI and ES animals.

Table 7. 5 Summary of EI (WD) and ES (WI) δ^{18}O medians across biomes with significance.

Biome	Most enriched in ^{18}O	ES vs. EI significance	WI vs. WD significance
Forest	Not sig different	p = 0.084	p = 0.770
Fynbos	ES	p = 0.002	p = 0.001
Succulent Karoo	ES	p = 0.039	p = 0.647
Nama Karoo	ES	p = 0.000	p = 0.894
Savanna	WI	p = 0.169	p = 0.001
Albany Thicket	ES/WD	p = 0.009	p = 0.014

In terms of which meteorological variables have the strongest relationship with the δ^{18}O values, the r^2 (adj) values for carnivores and primates were low. This indicates that meteorological factors are not a good predictor of δ^{18}O for these groups and that there are other factors responsible for δ^{18}O. This is not surprising since primates are known to be reliant on daily drinking water (Crowley, 2012; Moritz *et al*., 2012) and would thus be more influenced by changes in the meteoric water δ^{18}O rather than levels of evaporation or aridity. Therefore, values should change only if source water δ^{18}O changes across localities. In the Albany thicket in particular, values for primates could also be influenced by the animals obtaining a significant proportion of their water from succulents.

In general, browsers appear to be good environmental proxies, as with carbon dataset. The δ^{18}O values for ES browsers track meteorological variables best. MAPE and WD seem to be the best predictors for ungulate δ^{18}O, with r^2 (adj) values of 0.63 and 0.64, respectively. Since WD is a calculated field based on MAPE and MAP, the similarity is understandable. Ayliffe and Chivas (1990), Levin *et al*. (2006) and Murphy *et al.* (2007a) all used δ^{18}O of bioapatite as a proxy for environmental variables such as water availability and rainfall. Levin *et al*. (2006) compared ES animals with EI animals to track aridity and found that the bigger the difference between the δ^{18}O values of ES and EI animals, the more arid the environment.

One of the aims of this project was to investigate whether the Levin *et al*. (2006) aridity index, developed in the context of the East African summer rainfall region, could be applied to areas that receive rain in the winter months. The data from this project indicate that a variation of the aridity index does indeed apply to the winter rainfall zone of southwestern Africa. The difference in $\delta^{18}O$ between animals sensitive to evaporation levels and those insensitive to evaporation levels is highest in the hotter, drier localities. The difference between ES and EI animals (Figure 5.15) was largest in the Nama Karoo (difference between EI and ES medians is 4.8), moderate in the Albany Thicket (1.5) and Savanna (1.0), and lowest in the Succulent Karoo (0.5) and Forest (-1.1). Fynbos does not fit neatly into the grading of biomes as it falls in between the Nama Karoo and Albany Thicket, placing it on the arid/warm end of the spectrum. This somewhat surprising result could be due to the high levels of variability found within the Fynbos biome. The negative value for the Forest biome (ES was lower than EI) is not unexpected since this biome is particularly moist and the ES and EI animals would not have any difference in $\delta^{18}O_{enamel}$ values. Thus, levels of evaporation would be low, and the leaves eaten by ES animals would not be evaporatively enriched.

The difference between ES and EI for the Savanna biome was lower than expected considering it is a comparatively arid biome, with a MAP of 184 mm and a RH of 47.4. This difference may be because EI animals (those that should be relatively negative) from the Savanna included species such as the gemsbok and red hartebeest, which are not reliant on regular drinking and are more drought tolerant (unlike many other EI animals). These two species had high $\delta^{18}O_{enamel}$ values, reducing the difference between ES and EI.

The Fynbos biome had a bigger difference in $\delta^{18}O_{enamel}$ values between ES and EI animals than was expected. This may be due to the high climatic variability within this biome. Parts of the Fynbos biome are rather arid (such as the West Strandveld with a MAP of 309 mm) while others are much wetter (such as the Eastern Fynbos/Renosterveld with a MAP of 615 mm). More samples are required from individual pockets of this environmentally diverse biome to evaluate $\delta^{18}O_{enamel}$ by bioregion or even location, rather than biome. The fact that the cooler (Forest) and the winter rainfall (Succulent Karoo) biomes are the ones with the low difference between ES and EI is interesting and not unexpected. Levin *et al*. (2006) found that the lower the water deficit, the smaller the difference.

It is important to note that the $\delta^{18}O$ of the local meteoric water was not tested. Levin *et al*. (2006) measured an ‘enrichment factor’ – i.e. the enrichment in ^{18}O of ES and EI animals compared with local meteoric water. Obtaining local $\delta^{18}O_{water}$ values was outside the scope of this study and thus an enrichment factor could not be calculated. Instead, this study relies on measurements of the difference between ES and EI animals. The rain in the biomes that receive all or some rainfall in summer (Savanna, Nama Karoo, Albany thicket, Forest) comes from the eastern Indian Ocean. The $\delta^{18}O$ of this rainwater may be sufficiently different from that derived from the western Atlantic Ocean to cause a measurable difference between these two regions (van der Merwe, 2013). In future work on this topic, it would be valuable to have the $\delta^{18}O$ of source water to calculate enrichment factors.

This study shows that the difference between the average $\delta^{18}O$ values of water dependent/evaporation insensitive and water independent/evaporation sensitive animals increases with increased aridity. There are, however, some exceptions to this pattern, such as in the Fynbos. Higher resolution of the environmental diversity in this biome is required in order to better understand this inconsistency. The results are sufficiently promising that in the future it would be worth measuring the meteoric water values for different localities across the winter rainfall biome.

7.1.3 $\delta^{15}N_{collagen}$

As animal tissues are consistently more enriched in ^{15}N compared to their food sources, $\delta^{15}N_{collagen}$ increases with increasing trophic level. Thus, it was expected that carnivores would display the highest $\delta^{15}N_{collagen}$. This was true in five out of six biomes (Table 7.6). In two biomes (Nama Karoo and Succulent Karoo), there was only one carnivore in the sample, thus statistical hypothesis testing was not performed. In three of the remaining four biomes, the carnivores were significantly higher than the browsers. Trophic level enrichments could be approximated by subtracting the median value for grazers or browsers from the carnivore median. This is of course an approximation, since the carnivores would not necessarily have consumed these species of animals. The difference between the median values for carnivores and browsers in the Forest biome was high (4.5‰). This is towards the upper end of the range of trophic enrichment previously documented (DeNiro and Epstein, 1981; Schoeninger and DeNiro,1984; Sponheimer *et al.,* 2003b; Caut *et al.,* 2009), but within the range measured by Ambrose (1991) in the Great Rift Valley in East Africa. Ambrose and DeNiro (1986) reported enrichment of 5-6‰ among animals collected largely from highland savanna grassveld of East Africa. O'Connell *et al.* (2012) have suggested enrichment of up to 6‰ for humans, but the values for wild fauna in the current study were not as high as this.

Table 7. 6 Summary of trophic levels in each biome.

Biome	Most enriched in ^{15}N	$\delta^{15}N$ median of the carnivores	Carnivores significantly different from:		
			Browsers	**Grazers**	**Omnivores**
Forest	Carnivores	8.2 (n=6)	Yes	No	No
Fynbos	Carnivores	10.9 (n=14)	Yes	No	Yes
Succulent Karoo	Carnivores	15.2 (n=1)	N/A	N/A	N/A
Nama Karoo	Mixed feeders	10.8 (n=1)	N/A	N/A	N/A
Savanna	Carnivores	14.2 (n=8)	Yes	Yes	No
Albany Thicket	Carnivores	15.2 (n=2)	No	No	Yes

In the four biomes in which carnivore samples consisted of more than one individual, grazers were significantly lower than carnivores in only the Savanna biome (Table 7.5). The similarity between the values for grazers and carnivores in most biomes is probably because carnivores were not consuming the grazing species in the study. For example, the carnivores analysed in the Forest biome (bat-eared fox, caracal, genet, leopard, honey badger) do not consume the grazers in that same biome (hippopotamus and buffalo). It should be noted that caracal, bat eared fox, genet and honey badger do eat rodents of which many species are granivores which could give a C_4 (graxing) signal. Thus, trophic level differentiation was not necessarily expected. This does, however, emphasise the $\delta^{15}N_{collagen}$ variation within trophic levels and the need to exercise caution when categorising animals into such crude groupings as 'herbivore' and 'carnivore'. The fact that there were no differences between the $\delta^{15}N$ values for grazers and carnivores in the Fynbos biome may also indicate that it is smaller browsing animals (with significantly lower $\delta^{15}N_{collagen}$ values) that are preyed upon by the carnivores.

In the Albany Thicket, $\delta^{15}N_{collagen}$ values for the carnivores (one lion and one spotted hyena) were the most positive. This enrichment in ^{15}N is quite clearly due to the effects of trophic level. We would not expect to see a large enrichment in aardwolf or bat-eared foxes, which are insectivores, but it would be expected for lions and spotted hyenas. Although the significance of the differences between carnivores and grazers and browsers is uncertain due to low carnivore sample numbers, the trophic level difference between carnivores and browsers is 3.6, and between carnivores and grazers it is 3.8. These are within previously reported ranges (Sealy *et al*., 1987; Ambrose, 1991; Caut *et al*., 2008).

Ambrose and DeNiro (1986) suggested that $\delta^{15}N$ values of drought-tolerant animals, many of which are browsers, should be higher than those of animals that have to drink regularly, most of which grazers. Their model postulates that, since excreted urea is depleted in ^{15}N, and the degree of depletion increases with water stress, the body tissues of drought tolerant animals will be enriched in ^{15}N. This pattern was not supported in this dataset (Table 7.7). Four biomes showed no significant difference between the $\delta^{15}N$ values of browsers and grazers, and in the other two (Forest and Fynbos) grazers had more enriched values. Browsers (and indeed, most other animal groups) from the Forest and Fynbos biomes are significantly more depleted in ^{15}N when compared with those from other biomes.

Table 7. 7 Comparison of grazer and browser $\delta^{15}N$ medians across biomes with significance.

Biome	Grazer $\delta^{15}N$ median	Browser $\delta^{15}N$ median	Significance
Forest	8.8	3.7	$p = 0.021$
Fynbos	10.3	5.9	$p = 0.029$
Succulent Karoo	10.5	10.9	$p=1.000$
Nama Karoo	9 (n=1)	10.1	$p = 0.226$
Savanna	10.4	10.3	$p=1.000$
Albany Thicket	11.2	11.4	$p=1.000$

Environmental factors, especially aridity, are key determinants of $\delta^{15}N$ in both plants and animals. In this study, the $\delta^{15}N_{collagen}$ values of ungulates from wetter biomes (especially the Forest biome) were lower than those from arid ones (Savanna, Albany Thicket and Nama Karoo) (Table 7.8). The Fynbos biome lies in between with a median of 9.3. Herbivore metadata compiled by Kelly (2000) also found elevated $\delta^{15}N_{collagen}$ at drier locations (up to 2.4‰ more positive at the xeric locations). This is not only because of the elevated $\delta^{15}N$ in plants that grow in dry environments, but probably also to the metabolic adaptations of animals to survive in these environments.

Table 7. 8 $\delta^{15}N$ of ungulates showing differences across biomes.

Biome	N	Median $\delta^{15}N$	Mean $\delta^{15}N$	Std. Deviation
Forest	33	5.8	5.9	2.4
Fynbos	28	9.3	8.7	3.6
Succulent Karoo	65	10.7	10.4	2.5
Nama Karoo	15	11.2	10.9	1.7
Savanna	45	10.3	10.4	1.1
Albany Thicket	65	11.2	11.2	1.4

It was expected that $\delta^{15}N$ values would be more positive in ES/WI animals (Ambrose and deNiro 1986; Ambrose and deNiro 1987; Sealy *et al.*, 1987; Schoeninger and DeNiro 1984; Cormie and Schwartcz 1996; Kelly, 2000; Vanderklift and Ponsard, 2003). This was not the case for most biomes. The expected pattern was found only in the Nama Karoo, though the sample size was small. In the Forest biome, the opposite pattern was seen, with the median $\delta^{15}N$ value for EI/WD animals higher than for ES/WI (Table 7.9). It was notable that the patterning in nitrogen isotopes in relation to aridity/drinking behaviour was much less clear than the patterning in oxygen isotopes.

Table 7. 9 Summary of EI (WD) and ES (WI) $\delta^{15}N_{collagen}$ medians across biomes with significance.

Biome	Group most enriched in ^{15}N	Significance
Forest	EI/WD	p = 0.000
Fynbos	not significantly different	p = 0.062
Succulent Karoo	not significantly different	p = 0.660
Nama Karoo	ES/WI	p = 0.019
Savanna	not significantly different	p = 0.741
Albany Thicket	not significantly different	p = 0.792

It was also hypothesized that ruminants would have higher $\delta^{15}N_{collagen}$ values compared with non-ruminants because of digestion and absorption of rumen microbes (Sealy *et al.*, 1987). Only in the Forest biome was there a significant difference between the $\delta^{15}N$ values of ruminants and non-ruminants –and it was the non-ruminants that displayed higher $\delta^{15}N$ values. The non-ruminants in this biome consisted only of bushpig, which have previously been reported (Sealy *et al.,* 1987) to be enriched in ^{15}N compared with other animals from the same location. This may be linked to the diet of bushpigs, which includes plants such as roots, tubers and rhizomes, as well as some animal-based food such as earthworms and insect larvae (Skinner and Chimimba, 2005).

The correlations between $\delta^{15}N_{collagen}$ and meteorological factors were best for carnivores, with MAP (r^2 = 0.63) and MI (r^2 = 0.60) displaying the closest correlations. This means that $\delta^{15}N_{collagen}$ values of archaeological carnivores could be used to predict MAP and MI in the past, although not with a very high degree of confidence. This is in contrast to the much weaker correlations between ungulate $\delta^{15}N_{collagen}$ and meteorological factors, with significant r^2 values ranging between 0.24 and 0.32. When the category "ungulates" was narrowed to a single species (eland), the correlation remained poor (r^2 = 0.36). These relationships are considerably weaker than those reported in Australia, where several studies have investigated $\delta^{15}N_{collagen}$ of the *Macropus* genus along aridity gradients. Gröcke *et al*. (1997) plotted

Macropus $\delta^{15}N$ against annual rainfall and found an r^2 value of 0.53. Murphy and Bowman (2006) used water availability (annual actual evapotranspiration/annual potential evapotranspiration) correlated against kangaroo $\delta^{15}N$ and reported r^2 of 0.57. In North America, Cormie and Schwarcz (1996) found that only animals that consumed more than 10% C_4 (i.e. grazers) showed a robust relationship between $\delta^{15}N$ and MAP. Pate and Anson (2008) and Sealy *et al.* (1987) found that in their studies, there appeared to be a rainfall threshold of between 240 and 400 mm MAP, below which $\delta^{15}N_{collagen}$ values of fauna were elevated. There is considerable variability in these relationships, making it difficult to interpret faunal $\delta^{15}N$ (Makarewicz and Sealy, 2015; Smiley *et al*., 2015). It may be that in this study, landscape-scale patterning is obscured by localized variations in moisture availability. Even so, these results highlight the difficulty of interpreting faunal $\delta^{15}N$.

Earlier studies assumed $\delta^{15}N$ homogeneity amongst herbivores, which we now know not to be the case. Codron *et al.* (2012b) showed that there can be inter-individual differences of up to 3‰ across animal populations that cannot be explained by diet or trophic level effects alone. The differences may be due to variations in metabolic rate or other physiological differences at the level of individual animals. Although patterning in $\delta^{15}N$ is complex, some trends have emerged. Most notably, arid environments had higher $\delta^{15}N$ values when compared with wetter ones. Carnivores tracked certain meteorological variables fairly well and thus archaeological specimens could be used to predict meteorological aspects of past environments.

7.1.4 Conclusions common to several isotopes studied

This study reinforces several conclusions that have been drawn from other research. In some cases, using a single species rather than a group produces stronger relationships between isotopic values and meteorological variables. Researchers tend to group species together because of poor sample size per species, wanting to make more meaningful statistical conclusions. In this study, a regression model was run focussing on the eland (a browser and ES animal) and the red hartebeest (a grazer and EI animal). This test attempted to remove variation caused by different species being grouped together in the sample. The $\delta^{18}O$ of red hartebeest and the eland had significant relationships with most meteorological factors; however, there was a clearer signal for eland compared with the red hartebeest. Thus in this data set the $\delta^{18}O_{enamel}$ values of this evaporation-sensitive browser track meteorological variables better. The eland $\delta^{18}O_{enamel}$ had the strongest relationship with WCR. In the case of the red hartebeest, the strongest relationship was with MAPE. For $\delta^{13}C_{collagen}$, it was the red hartebeest that showed a strong correlation between its $\delta^{13}C$ and SAI (r^2 = 0.62). A larger sample size generated by collecting over a longer time period or a bigger area would increase our confidence in these relationships. It should be noted again that the eland's diet selectivity could be driving some of the variance seen in the $\delta^{13}C$.

A second common conclusion was that using a single meteorological factor was adequate for these isotopes. Multiple regression models run for the $\delta^{13}C$, $\delta^{18}O$ or $\delta^{15}N$ for ungulates, carnivores and primates did not yield improved correlations by much, if at all. For example, the regression model using only MAT (in the case of $\delta^{13}C_{enamel}$ for ungulates) yielded a correlation of 0.75 (r^2 adj). When a more complicated regression model was run including two variables (RH and SAI), the r^2 did not change. For $\delta^{18}O$, the model with only MAPE had an r^2 value of 0.63 while the more complex model using MAPE and WCR resulted in the marginally improved r^2 value of 0.64. In some cases, the use of multiple variables led to a smaller r^2 value (the carnivore subset correlated with WCR alone had an r^2 value of 0.57 ($p<0.001$) and the r^2 using two variables was only 0.42). Thus, results of the regression models in this study suggest that more complex models incorporating several meteorological factors did not add value to the models. Similar studies should keep this in mind since running additional models may not yield a more robust result.

The final common conclusion is that primates showed poor relationships with all meteorological factors. For all of the isotopes measured in this project, the r^2 values for primates were low, indicating that the environmental variables were not a good predictors of $\delta^{13}C$, $\delta^{18}O$ or $\delta^{15}N$. Thackeray *et al*. (1996) have also found no clear association between primate $\delta^{15}N$ (*Papio ursinus*, the chacma baboon) and meteorological factors, particularly rainfall. There are other factors responsible for the change in isotopes. Primates (especially baboons, which make up a large proportion of this primate sample) are intelligent, adaptable and eat a wide range of foods. Thus, the behaviour of baboons is likely to change with climate and they may not be good animals for these types of studies.

7.2 Intra-individual variation in isotope values

Studies by archaeologists and palaeontologists are limited by what survives in archaeological and fossil deposits. In older sites, it is often the enamel apatite (rather than bone or dentine collagen) that survives. There is no way of predicting which teeth (e.g. M1, M2 or M3) will be found. Thus, it is important to understand the relationship of stable isotope values in teeth along the tooth row of one individual as well as the relationship between the isotope values of bone collagen and enamel apatite.

7.2.1 Tooth row

Changes in the $\delta^{13}C_{enamel}$ along the tooth row reflect changes in diet over the time period of mineralization. This study found that although there were changes along the tooth row, there was no systematic offset of one or more teeth in any particular direction. In the ungulate dataset, the M1s were not always more depleted in ^{13}C than the other molars. This contradicts a widely-cited previous study, in which the M1 was found to have more negative $\delta^{13}C_{enamel}$ than M2 and M3 (Zazzo *et al.,* 2002). That study, however, was based on only five animals. The current study reports values for all three molars for 22 animals (excluding the *Oryx gazella*, or gemsbok, known to have undergone changes of residence and therefore diet). This study more than quadruples the sample size of Zazzo *et al*. (2002) and provides clear evidence that, for the animals of interest here, choice of molar tooth for analysis does not lead to systematic biases in the $\delta^{13}C_{enamel}$ values measured.

The amount of variation in $\delta^{13}C_{enamel}$ along the tooth row depends upon two main aspects: whether the diet includes only C_3 or also C_4 foods, and (to a lesser extent) whether there are marked seasonal variations in the $\delta^{13}C$ values of the C_3 plants. Studies by Zazzo *et al.* (2002) and Wang *et al.* (2008) both analysed teeth from C_3 environments, and found variations along the tooth row of up to 1.9 and 4.8‰ respectively. Balasse *et al.* (2002) studied experimental animals whose diets were switched from pure C_3 to include C_4 foods; not surprisingly, they saw much larger changes. In the current study, some species (e.g. *Raphicerus campestris*, steenbok) showed greater variation in $\delta^{13}C_{enamel}$ along the tooth row (up to 4.1‰) than others (e.g. *Tragelaphus strepsiceros,* kudu: range of up to 2.3‰). The former has a more variable diet, which may include both graze and browse, while the latter strongly favours browsing. The most variable values were for *Oryx gazella* (gemsbok) but, as described in Chapter 5, these animals underwent residential and dietary changes during their lifespans.

Variation in $\delta^{18}O_{enamel}$ reflects seasonal variations in water $\delta^{18}O$. Previous authors have also suggested that early-forming teeth (pre-weaning) have high $\delta^{18}O$ values because metabolic processes lead to body water becoming enriched in ^{18}O relative to drinking water (e.g. Bryant and Froelich, 1995). This enrichment is passed on to suckling infants. Fricke and O'Neil (1996) reported that in sheep, the $\delta^{18}O$ values of the first molar were 1.5-3‰ higher than the second or third molars of the same animal. Zazzo *et al.* (2002) found M1s to be more enriched in ^{18}O than M2s, although M3s frequently showed relatively positive values, similar to M1s. This systematic inter-tooth patterning is not evident in this study. There are no consistent differences between the $\delta^{18}O_{enamel}$ values of first, second and third molars. This may be because the wild animals studied here suckle less than domesticated sheep or cows. It may also be that seasonal shifts in the $\delta^{18}O$ of drinking water and/or food, and possible variation in season of birth, are large enough to make any weaning signal undetectable. Murphy *et al.* (2007a) also did not find consistent offsets between kangaroo molars and concluded that the weaning effect was either absent or invisible, given seasonal variation in $\delta^{18}O$ of precipitation.

This study found variations in $\delta^{18}O_{enamel}$ along the tooth row of up to 6.2‰. Wang *et al.* (2008) reported inter-tooth variations of up to 10.8‰, while Zazzo *et al.* (2002) documented inter-tooth differences of only up to 3.7‰. In this study, some species such as the springbok, blue duiker and common duiker had very similar $\delta^{18}O$ values along the tooth row; all except for one specimen had ranges <2.5‰. Among others, such as the two *Raphicerus* species, the variation was much larger (up to 6.2‰).

While the dataset collected for this thesis shows that $\delta^{13}C_{enamel}$ and $\delta^{18}O_{enamel}$ values can vary quite substantially along the tooth row, there was no evidence of systematic off-sets between the different teeth. This variation needs to be taken into account in archaeological and palaeontological studies, which frequently and unavoidably rely on only a small number of samples. The data collected here allow for an assessment of between-sample differences in $\delta^{13}C$ and $\delta^{18}O$ in the context of the degree of intra-individual variation. The hope is to avoid over-interpretation of small differences that may simply reflect natural variation.

7.2.2 Relationship between $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$

In this study, correlations between $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$ were significant for all three main animal groups: ungulates (r^2=0.77), carnivores (r^2=0.66) and primates (r^2=0.69). Loftus and Sealy (2012) reported a similar correlation (r^2= 0.71) between $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$ for archaeological humans from the southwestern Cape.

In the current study, carnivores had the smallest $\Delta_{enamel\text{-}collagen}$ with a median of 5.0‰ (mean 4.6 ± 1.9‰), ungulates had the largest spacing (median 7.1‰; mean 7.3 ± 2.3‰), and primates fell in between (median 5.5‰; mean 5.5 ± 1.2‰). Ungulates were significantly different from both carnivores and primates. This is the expected pattern based on models in the literature. Due to their high protein diet, carnivores are expected to route more carbon from the amino acids in their diet to their proteinaceous tissues, while herbivores, having low protein diets, are expected to synthesize more non-essential amino acids, incorporating carbon from dietary carbohydrates and lipids as well as protein (Hedges, 2003; Crowley *et al.*, 2010). Herbivore and carnivore $\Delta_{enamel\text{-}collagen}$ should thus be distinguishable, with herbivores having a larger spacing ($\Delta_{enamel\text{-}collagen}$) than carnivores. This pattern is observed in this study, with values for $\Delta_{enamel\text{ -}collagen}$ very similar to those reported by Lee-Thorp *et al*. (1989), who found mean $\Delta_{enamel\text{-}collagen}$ was 6.8 ± 1.4‰ for herbivores, 5.2 ± 0.1‰ for omnivores and 4.3 ± 1.0‰ for carnivores. It should be noted that many apatite values in the Lee-Thorp *et al*. (1989) study were for bone apatite, whereas this study reports values only for enamel apatite, which is slightly enriched in ^{13}C relative to bone apatite (Warriner and Tuross, 2009; Webb *et al.,* 2014). Taking this into consideration, the agreement between the two studies is remarkably close.

The larger $\Delta_{enamel-collagen}$ spacing in ungulates (herbivores) may be related to methanogenesis and/or protein source: plant protein for herbivores, animal protein for carnivores (Lee-Thorp *et al.*, 1989).

When looking at the dataset broken down by biome, the Forest biome had the lowest $\Delta_{enamel-collagen}$ for ungulates. The sample numbers became very low after separating by biome, so these results may not be as robust as the overall values. The ungulate $\Delta_{enamel-collagen}$ median was 6.3 for Forest, which was significantly lower than Savanna at 8.7 (p<0.001) and also Albany Thicket at 7.6 (p=0.014), respectively. For carnivores, the Savanna (median = 3.1) and the Forest biome (median = 3.4) had the lowest $\Delta_{enamel-collagen}$. For primates, the median $\Delta_{enamel–collagen}$ was the lowest in the Forest (5.0) and the Fynbos (5.5) biomes which are both significantly lower than the more arid Succulent Karoo (p=0.005 and 0.024, respectively). In Australia, Murphy *et al.* (2007) showed that the $\Delta_{apatite-collagen}$ increased with aridity. The current dataset also suggests that water availability may be an important factor, since the Forest biome, with the greatest water availability, had low $\Delta_{apatite-collagen}$ spacings for ungulates and primates (but not carnivores).

Hedges (2003) predicted that ruminants should have larger $\Delta_{apatite-collagen}$ spacings. This is because they excrete significant quantities of ^{13}C depleted methane, which leads to ^{13}C enriched blood bicarbonate (and hence bone and tooth apatite). In this study, $\Delta_{enamel-collagen}$ values were indeed found to be significantly larger in ruminants than non-ruminants (ruminant median = 7.2, mean 7.4 ± 2.3‰, n=169; hindgut/non-ruminant median = 6.0, mean 6.0 ± 1.6‰, n=23; p=0.002). This finding supports Hedges' (2003) prediction by providing the first clear evidence from a field study that gut physiology does indeed affect $\Delta_{apatite-collagen}$ spacing.

The comparison of grazers/browsers shows that grazers have bigger $\Delta_{enamel-collagen}$ (median = 8.6, mean 8.4 ± 2.4‰, n=101) compared with browsers (median = 6.2, mean 6.4 ± 1.9‰, n=94). This is in contrast to a controlled feeding study by Hare *et al.* (1991) that reported a spacing of 9.1 for a C_3 diet (browsers) and 6.8 for a C_4 diet (grazers).

The median $\Delta_{enamel-collagen}$ values were also compared by body size. The $\Delta_{enamel-collagen}$ spacing was larger in bigger animals ('Large' = 8.5, 'Medium' = 6.4 and 'Small' = 5.9). As far as I am aware, no other researchers have looked at wild faunal data in this way. Kellner and Schoeninger (2007) analysed previously published datasets from feeding studies. They concluded that the protein source (either C_3 or C_4) was the major determinant of the spacing. It should be noted that they compared bone apatite and bone collagen. In this study, the $\Delta_{enamel-collagen}$ values were also bigger for EI (median of 8.4) as opposed to ES animals (median of 6.5). However, the EI group contained 91 "Large" animals, while the ES group had only 32

"Large" animals. All the "Small" animals were ES. Looking back at the ruminants as well as the grazing groups, they are also mostly larger animals. While Kellner and Schoeninger (2007) have argued that protein source is a more important influence than body size, the current dataset indicates that although the protein source (i.e. C_3 or C_4 plants) does have a good correlation, the body size is a better fit. In this dataset it is the body size groups that provide the best correlation between $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$. This is an avenue for future exploration.

In summary, this study contributes to isotopic studies investigating the difference between tissues of the same individual (Warinner and Tuross, 2009; Loftus and Sealy, 2012; Webb *et al.* , 2014; Santana-Sagredo *et al.,* 2015a). The $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$ correlated well for most animal groups. Difference between $\delta^{13}C_{enamel}$ and $\delta^{13}C_{collagen}$ ($\Delta_{enamel\text{-}collagen}$) supported published studies, with ungulates having the highest value and carnivores the lowest. Large ungulates and ruminants were found to have a larger $\Delta_{enamel\text{-}collagen}$ spacing, probably due to the increased excreted methane.

7.3 Applications to palaeo studies and avenues for future research

7.3.1 Comparison of archaeological datasets with the modern baseline

The dataset presented in this thesis can be used as a modern baseline to better interpret archaeological isotopic datasets. By comparing previously published $\delta^{13}C_{enamel}$ and $\delta^{18}O_{enamel}$ archaeological data with modern datasets, archaeological sites can be placed within a modern environmental context.

For example, Figure 7.1 graphically presents $\delta^{13}C_{enamel}$ isotopic values from this study (corrected for the fossil fuel effect) from browsers and grazers from the Fynbos biome and compares them with published data from the paleontological sites Elandsfontein, Hoedjiespunt and Langebaanweg (Luyt *et al.*, 2000; Franz-Odendaal *et al.*, 2002; Hare and Sealy, 2013; Lehmann *et al*., 2016). As noted above, in this region the isotope values of browsers are the best environmental proxies, so this interpretation is based upon browsers. $\delta^{13}C_{enamel}$ values of modern browsers in the Fynbos biome are significantly different from only Hoedjiespunt (Kruskal-Wallis H (3) = 19.074, $p < 0.001$). The deduction from the current data is that the environment at Hoedjiespunt at the time of deposition differed from that of the Fynbos biome today. The median $\delta^{13}C_{enamel}$ value for browsers at Hoedjiespunt is -10.1‰, which is 2.6‰ higher than the median for the modern Fynbos (-12.7‰). Based on the data in this thesis, the regression results for $\delta^{13}C_{enamel}$ versus MAT, could be used to suggest that the MAT at Hoedjiespunt was 1.1 degree Celsius higher than it is today.

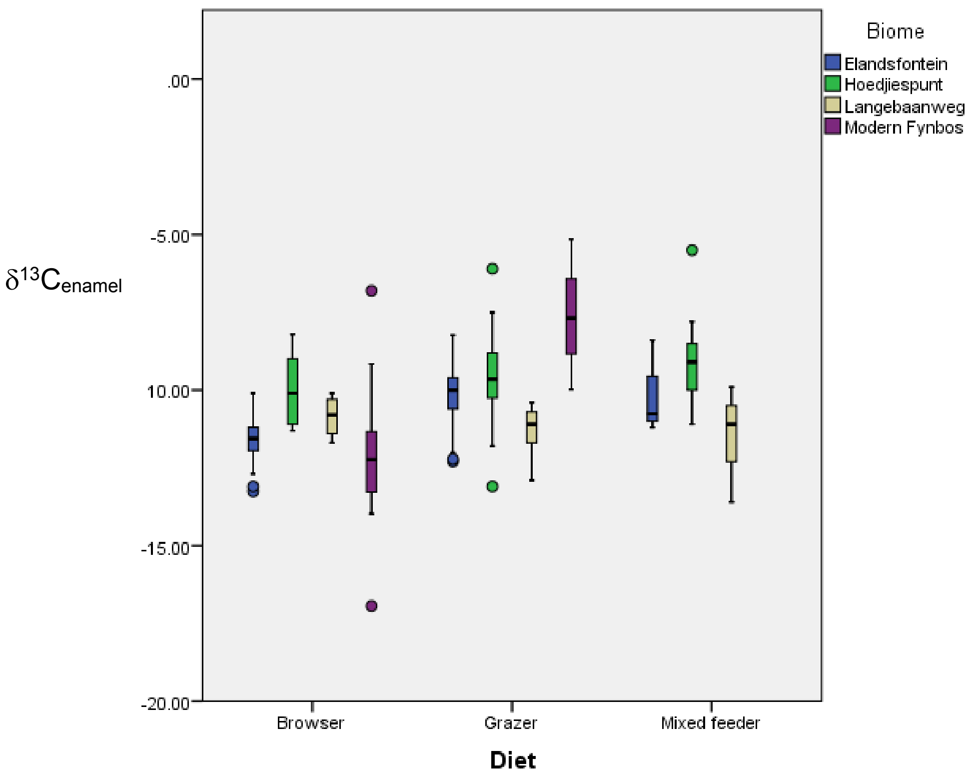

Figure 7. 1 $\delta^{13}C_{enamel}$ for fauna from the archaeological sites of Elandsfontein, Hoedjiespunt and Langebaanweg compared with values for the modern Fynbos biome (with 2.0‰ added to correct for the fossil fuel effect: Keeling *et al.,* 2009; Bocherens *et al.* , 2014) plotted by ungulate dietary preference.

$\delta^{13}C_{enamel}$ values from Elandsfontein (*p* = 0.100) and Langebaanweg (*p* = 0.263) were not significantly different from the modern Fynbos. This does not, of course, mean that the environments at Elandsfontein and Langebaanweg were the same as the modern Fynbos (or the same as each other), merely that they cannot be distinguished in terms of browser $\delta^{13}C_{enamel}$. Since there were only three modern grazers from the Fynbos biome, comparison with archaeological assemblages is not robust.

The $\delta^{18}O$ values of browsers in the modern Fynbos dataset were significantly different from only one archaeological dataset, the Langebaanweg browsers (*p* = 0.004) (Kruskal-Wallis H (3) = 17.377, *p* = 0.001), indicating that the $\delta^{18}O$ value of surface water and/or the environment was different. Browsers from Langebaanweg were also significantly different from Elandsfontein (*p* = 0.003), with the $\delta^{18}O$ values from Langebaanweg approximately 4.5‰ more negative than those from Elandsfontein (Lehmann *et al.*, 2016). Only the suids did not differ at the two sites.

The substantial difference in $\delta^{18}O$ at Langebaanweg is attributed to a difference in the $\delta^{18}O$ of the surface water available for animals to drink at this much earlier time (Lehmann *et al.*, 2016). Langebaanweg is dated to around 5 million years ago while Elandsfontein is dated to between 1 million and 600 000 years ago. The late Miocene to Pleistocene was a time of aridification in Africa, and the surface water at Elandsfontein would have been subjected to higher levels of evaporation. This does not, however, explain the entirety of the shift. Regional circulation patterns that determine the origin of the rain and local hydrology may have been different in the Miocene. These circulation patterns appear to have been relatively stable from the Pleistocene to the present, based on the $\delta^{18}O$ of hippopotamids which track local meteoric water (Bocherens *et al.*, 1996). Taking fractionation into account, the $\delta^{18}O$ of hippopotamids from Elandsfontein indicate water with $\delta^{18}O$ very similar to that of contemporary surface water (Lehmann *et al.*, 2016).

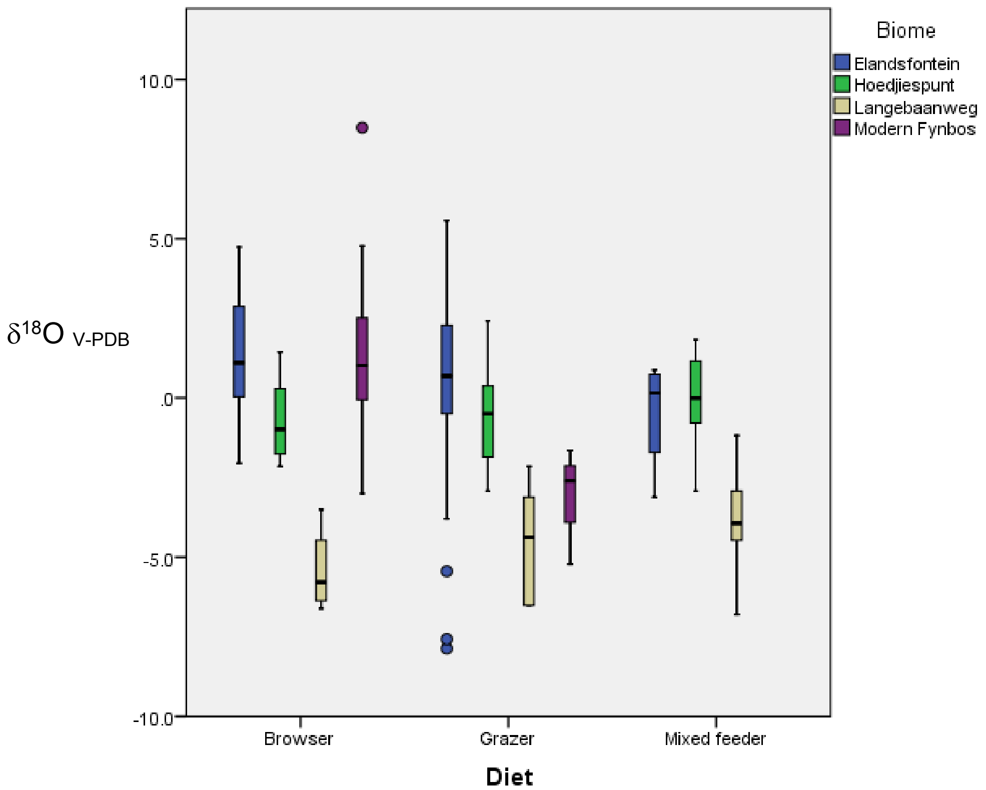

Figure 7. 2 $\delta^{18}O_{enamel}$ for fauna from the archaeological sites of Elandsfontein, Hoedjiespunt and Langebaanweg compared with values for the modern Fynbos biome plotted by ungulate dietary preference.

7.3.2 Using $\delta^{18}O$ values as a measure of aridity to better interpret archaeological assemblages

The difference between the median $\delta^{18}O$ value of EI and ES animals varied across the biomes. The difference was greater in more arid areas, as found by Levin *et al.* (2006). They reported that the $\delta^{18}O$ of EI animals tracked the $\delta^{18}O$ of the local water while the $\delta^{18}O$ of ES animals increased with aridity. They also found that the difference between the two groups increased with increased aridity. In the current dataset, the Nama Karoo, with MAP of 203 mm and RH of 63%, shows the largest difference between the medians for EI and ES animals (Figure 7.3). At the other end of the spectrum lies the Forest biome, where ES animals have lower $\delta^{18}O$ values than their EI counterparts. Here, evaporation is low enough that evaporative enrichment of leaves is negligible.

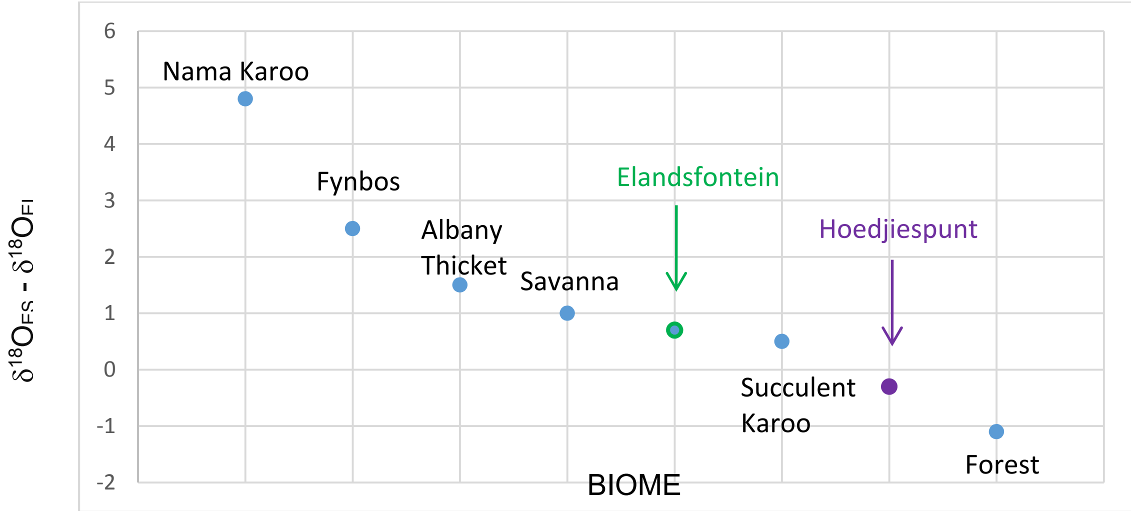

Figure 7. 3 A measure of aridity for Hoedjiespunt and Elandsfontein archaeological sites overlaid on the contemporary baseline "aridity index" of this study.

A similar calculation was done for Hoedjiespunt, using data from Hare and Sealy (2013), and for Elandsfontein, using data from Lehmann *et al.* (2016) and Luyt *et al*. (2000). All browsers were categorised as ES and all grazers as EI. The difference between the median values for Elandsfontein was 0.7, which is in the range between the modern (very arid) Savanna and Succulent Karoo biomes. Lehmann *et al.* (2016) also calculated an aridity index from the Elandsfontein data but used only two species – one representing the lowest $\delta^{18}O$ values (Hippopotamid) and the other representing the more evaporatively enriched values (Giraffids). Since Hippopotamus specimens are aquatic, and thus have $\delta^{18}O$ values similar to source water, an approximate value could be calculated for the local meteoric water. The index according to their calculation was 2.7 ($\pm$1.9), which would put it in a much more arid position on the modern continuum represented in Figure 7.3. The value of -0.3 for Hoedjiespunt places it near the modern Forest biome. Hoedjiespunt (dated to between 240 000 and 40 000 years old) seems to have been a wetter environment than Elandsfontein (between 600 000 – 1 000 000 years ago). More samples from these sites are required to determine the degree of aridity with greater confidence, and this should be a focus of future work. If hippopotamid values were available from archaeological sites, a value for meteoric water could be approximated and more accurate enrichments could be calculated.

Using $\delta^{18}O$ and $\delta^{13}C$ in tandem like this allows the researcher to discriminate between various possible explanations for the shifts observed. For example, the more positive $\delta^{13}C_{enamel}$ values seen at Hoedjiespunt might, on their own, be attributed to either warmer or drier conditions. In combination with the $\delta^{18}O$ values, however, higher MAT becomes the better explanation.

7.4 Conclusion

This study set out to develop a comparative modern dataset to allow for more precise interpretation of palaeo-environmental data. This study highlights the fact that relationships between stable isotope ratios in fauna and climatic variables exist, but that these relationships are stronger in certain animals than in others.

Based on the sample of animals assembled for this thesis, it was found that red hartebeest $\delta^{13}C_{collagen}$ had the closest relationship with environmental variables SAI and WCR, while $\delta^{13}C_{enamel}$ values of the ungulate group had the closest relationship with SAI, WCR and MAT. The fact that SAI and WCR were highly correlated with carbon isotope values is not surprising, given that both are indices of rainfall seasonality. Carnivore $\delta^{15}N$ was found to track meteorological variables more closely than any of the herbivore groups, presumably because animals at higher trophic levels are better integrators of their environments. Primates, on the other hand, were found to show poor relationships between $\delta^{13}C_{enamel}$, $\delta^{13}C_{collagen}$, $\delta^{18}O_{enamel}$, $\delta^{15}N_{collagen}$ and meteorological variables. $\delta^{18}O$ of eland was significantly positively correlated to all meteorological variables (highest r^2 was for WCR), with better correlations than any of the other species or groups. Future research should focus on obtaining better sample numbers so that these species can be confirmed as the best indicator species or others can be identified. Eland are found in many archaeological sites and if it is confirmed as a best indicator species with more contemporary samples, the eland $\delta^{18}O$ could thus be used to infer WCR at the time of deposition. The data set presented here could be improved by including more animals collected over a longer period of time, including wet years and dry years, in order to better characterise isotopic variability across environmental gradients.

The difference between $\delta^{13}C$ of enamel apatite and bone collagen ($\Delta_{enamel\text{-}collagen}$) was larger in herbivores than in carnivores or omnivores. It was also larger in ruminants than non-ruminants, probably due to methanogenesis.

Results of the regressions of isotope values and meteorological factors suggest that simple models based on single meteorological factors are just as good as more complex models, and that incorporating several meteorological factors does not add value. For each of the isotope studied ($\delta^{13}C_{enamel}$, $\delta^{13}C_{collagen}$, $\delta^{15}N$ and $\delta^{18}O$), regressions against individual meteorological factors had r^2 values similar to or higher than more complex models.

This dataset provides a unique perspective for interpreting and better understanding aspects of past environments and animal adaptations. It documents, for the first time, natural variation in stable C, N and O isotopes in animals from the C_3 Fynbos winter rainfall biome of South Africa. This can be used to identify climatic shifts in the past. The study provides a substantial amount of information on isotope values along the tooth-row and in tooth and bone from the same animal. These findings are relevant not only to the winter rainfall zone of South Africa, but to the larger and rapidly growing field of large mammal stable isotope studies. Finally, this thesis includes a preliminary exploration of how modern data can be applied to the interpretation of patterning in the $\delta^{13}C$ and $\delta^{18}O$ values of archaeological and palaeontological assemblages.

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APPENDICES

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CAPE RESEARCH CENTRE
P.O. Box 216, STEENBERG, 7947
Tel: +27 (0)21 713 7511; Fax: +27 (0)21 712 0131

Research Permit: 19 May 2014
AUGRABIES FALLS, ADDO ELEPHANT, AI-AIS/RICHTERSVELD TRANSFRONTIER, BONTEBOK, GARDEN ROUTE, KALAHARI GEMSBOK, KGALAGADI, NAMAQUA, TABLE MOUNTAIN, TANKWA KAROO and WEST COAST NATIONAL PARKS

Ms Julie Luyt - "**An application of light stable isotope biogeochemistry to shed light on the environmental changes in the southern African Winter and all-year rainfall zones**"
Co-workers: Judith Sealy, Lesa Swart and Deano Stynder
Department of Archaeology, University of Cape Town, Private Bag X3, Rondebosch 7700

Herewith the permit for your research project valid from **19 May 2014** until **31 March 2015**. The approval is subject to the following conditions. The Park Management staff must be contacted prior to entry into the park (see list of staff members below). You are allowed access to **All Areas** of the parks.

Standard Conditions:

- Please note that you (your delegates, staff etc) are subject to the conditions set in terms of Section 86(1) of the National Environmental Management Act (107 of 1998) and the National Environmental Act: Protected Areas Act (Act 57 of 2003) for the duration of your stay in the National Park. Your attention is specifically drawn to sections 64(1) (a), (b) & (c) which refers to penalties in terms of the Act.
- The areas under the control of SANParks are used entirely at your own risk and SANParks shall not be liable for any claims, accidents, injuries or loss, etc. arising from such use.
- No damage shall be permitted to any natural vegetation, environment or property. Any damage done shall be made good at your expense. Strictly no fires, smoke machines or audible generators will be permitted. No braais or skottels allowed unless in dedicated braai areas. NO LITTERING. Please take all rubbish away with you.
- Your permit must be retained and kept on your person at all times, and produced on request.
- Only open access pathways and roads are permitted to be used, unless by special arrangements.

Please contact the park management staff if restricted areas need to be accessed. No parking shall be permitted in entrances to access roads.

- SANParks staff's instructions shall be complied with. Visitors to the area may not be hindered in any way. The research activity shall be restricted to the area applied for.

Special Conditions:

- The researcher will collect dead animals (particularly the teeth) of identified fauna (List below). Whole carcasses may not be removed. Only the skull with teeth embedded in bone may be removed
- Researcher will walk into the field to collect the dead animal, if not collected by rangers at a central place.

Park - Area	Park Management Staff	Telephone Number:
Ai/Ais Richersveld	Nick de Goede	027 831 1506
AENP	Ane Oosthuizen	083 5408200
AFNP	Frans van Rooyen	(0)54 452 9200
BNP	Roland January	028 514 2735
GRNP	Jessica Hayes	044 343 1302
KGNP	Steven Smith	054 561 2003
NNP	Bernard van Lente	027 672 1948
TKNP	Conrad Strauss	027 341 1927
TMNP - CoGH	Justin Buchman	021 780 9100
TMNP - Silvermine	Leighan Mossop	021 789 2457/2404
TMNP - Tokai	Sandra Hollermann	021 712 2337/2884
TMNP - Table Mountain	Jannie du Plessis	021 402 2803/1601
WCNP	Pierre Nel	022 772 2144

Yours faithfully,

Signature Removed
Debbi Winterton - Science Liaison Officer; E-mail: deborah.winterton@sanparks.org

List of targeted species

Species - Herbivores	**Common name**	**Species - Herbivores**	**Common name**
Alcelaphus buselaphus	Red Hartebeest	*Histrix Africa-australis*	Porcupine
Antidorcas marsupialis	Springbok	*Otocyon Megalotis*	Bat-eared Fox
Cephalophus monticola	Blue duiker	*Herpestes*	Yellow Mongose
Damaliscus dorcas dorcas	Bontebok	*Struthio camelus*	Ostriches
Oreotragus oreotragus	Klipspringer	*Petromus typicus*	Dassie rat
Pelea capreolus	Rhebok grey	*Procavia capensis*	Rock dassie
Raphicerus campestris	Steenbok	*Equus zebra hartmannae*	Zebra hartmann's
Raphicerus melanotis	Cape Grysbok	*Equus zebra zebra*	Cape Mountain Zebra
Sylvicapra grimmia	Grey/Common Duiker	*Equus burchelli*	Burchell's/Plains zebra
Taurotragus oryx	Eland	*Papio Ursinus*	Chacma Baboon
Redunca fulvorufula	Mountain Reedbuck	*Loxodonta africana*	African elephant
Tragelaphus scriptus	Bushbuck	*Cercopithecus pygerythrus*	Vervet monkey
Oryx gazelle	Gemsbok	*Potamochoerus larvatus*	Bushpig
Tragelaphus strepsiceros	Kudu	*Phacochoerus africanus*	Warthog
Syncerus caffer	Buffalo	*Hippopotamus amphibius*	Hippo
Lepus capensis		*Connochaetes taurinus*	Blue Wildebeest
Species - Carnivores	**Common name**	**Species - Carnivores**	**Common name**
Otocyon megalotis	Bat-eared Fox	*Felis silvestris lybica*	African Wild Cat
Canis mesomelas	Black-backed Jackal	*Poecilogale albinucha*	African Striped Weasel
Hyaena brunnea	Brown Hyena	*Lycaon pictus*	African Wild Dog
Panthera pardus	Leopard	*Orycteropus afer*	Antbear (Aardvark)
Panthera leo	Lion	*Crocuta crocuta*	Spotted Hyena
Caracal caracal	Caracal	*Vulpes chama*	Silver (Cape) Fox
Acinonyx jubatus	Cheetah	*Felis nigripes*	Small Spotted Cat
Suricata suricatta	Suricate	*Ictonyx striatus*	Striped Polecat

Western Cape Province

Telephone No: (027) 021 483 0000
EMail: permits.fax@capenature.co.z
PGWC Shared Services Centre
cnr Bosduif and Volstruis Streets
Bridgetown
7764

CapeNature

Facsimile No: (027)0865567734
Internet: www.capenature.co.za
Private Bag X29
Gatesville
7766

PERMIT TO HUNT WITH
PROHIBITED HUNTING METHOD OF WILD ANIMALS - RESEARCH PURPOSES

(Issued in terms of the provisions of the Nature Conservation Ordinance 1974, (Ord 19 of 1974)Section29&33)

Not Transferable

Holder

Full Name	Ms J Luyt	**Identity No.**	7512060069082
Trade Name	University of Cape Town	**Registration No.**	AAA007-01802
Postal Address	Private Bag X3	**Physical Address**	NA
Suburb\Town	Rondebosch	**Suburb\Town**	NA
Province\State	Western Cape	**Province\State**	
Country	South Africa	**Country**	
Postal\Zip Code	7701	**Longitude**	.0000
		Latitude	.0000

In terms of and to the provisions of the abovementioned Ordinance and the Regulations framed thereunder, the holder of this permit is hereby authorised to Hunt (capture/disturb/stampede/kill) the protected wild animal(s) specified below on the property mentioned on this permit. See conditions on last page:

Details

Permit/Licence No	**0056-AAA007-00059**	*Stamp:* CapeNature FAUNA • FLORA • HUNTING • CITES
Expiry Date	31/12/2014	
Date Issued	19/04/2013	
Amount Paid	R 0.00	
Reference	NA	
File Code	1/2/1/6/5/F6	

Description	Property
Organization	University of Cape Town
Person	Luyt J Ms
ID	7512060069082
Properties	NA
Physical Address	Within the Western Cape Province only.
District	NA
Province/State	Western Cape
Country	South Africa
Longitude	.0000
Latitude	.0000

Species(Scientific Name)	Qty	Note
Bat-eared fox(Otocyon megalotis)	0	Unlimited - teeth.
Blue Duiker(Cephalophus monticola)	0	Unlimited - teeth.
Bontebok(Damaliscus pygargus pygargus)	0	Unlimited - teeth.
Bushbuck(Tragelaphus scriptus)	0	Unlimited - teeth.
Cape grysbok(Raphicerus melanotis)	0	Unlimited - teeth.
Chacma Baboon(Papio ursinus)	0	Unlimited - teeth.
Common duiker(Sylvicapra grimmia)	0	Unlimited - teeth.
Dassie rat(Petromus typicus)	0	Unlimited - teeth.
Eland(Taurotragus oryx)	0	Unlimited - teeth.
Gemsbok(Oryx gazella)	0	Unlimited - teeth.
Grey rhebok(Pelea capreolus)	0	Unlimited - teeth.
Klipspringer(Oreotragus oreotragus)	0	Unlimited - teeth.
Kudu(Tragelaphus strepsiceros)	0	Unlimited - teeth.
Mongoose, Small Grey(Herpestes pulverulenta)	0	Unlimited - teeth.
Ostrich(Struthio camelus)	0	Unlimited - teeth.
Plains zebra(Equus quagga)	0	Unlimited - teeth.
Porcupine(Hystrix africaeaustralis)	0	Unlimited - teeth.
Red hartebeest(Alcelaphus buselaphus)	0	Unlimited. Skull with teeth.
Rock dassie(Procavia capensis)	0	Unlimited - teeth.
Springbok(Antidorcas marsupialis)	0	Unlimited. Skull with teeth.
Springhare(Pedetes capensis)	0	Unlimited - teeth.
Steenbok(Raphicerus campestris)	0	Unlimited - teeth.

Signature Removed

Issued by:
Lee-Anne Benjamin Western

19/04/2013
Effective Date

Signature of Holder
I acknowledge, accept and understand fully the permit conditions as described

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Standard Conditions

1. When the holder of this permit *kills/captures/collect any wild animal in terms thereof, he shall, before leaving the above-mentioned property, or if he does not leave it, after each day's *hunt/capture/collection, record the particulars regarding the date, species and number of each sex of each species, or if it is impossible to distinguish the sex, the total number of each species of such wild animals which he had *killed/capture/collected.

2. The holder of this permit shall return it to the Chief Executive Officer: Western Cape Nature Conservation Board, Private Bag X29, Gatesville, 7766, within 14 days of the date of expiry thereof.

3. THIS PERMIT IS SUBJECT TO THE ADDITIONAL CONDITIONS AS SET OUT IN THE ADDENDUM HERETO.

Special Conditions

Method of capture:
Only interested in dead remains.

Number of persons engaged in this project:
Julie Luyt: PhD student.

CONDITIONS APPLICABLE TO RESEARCHERS UNDERTAKING RESEARCH OR OTHER COLLECTING WORKS ON PROVINCIAL CONSERVATION AREAS AND / OR PRIVATELY OWNED LAND IN THE PROVINCE OF WESTERN CAPE:

1. THE MANAGER OF THE RELEVANT CONSERVATION AREA(S) (IF ANY) MUST BE INFORMED TIMEOUSLY BEFORE ANY CONSERVATION AREA IS ENTERED FOR COLLECTING OR RESEARCH PURPOSES AND THE MANAGER'S WRITTEN PERMISSION TO ENTER SUCH RESERVE MUST BE ACQUIRED BEFOREHAND. THIS PERMIT DOES NOT GRANT THE PERMIT HOLDER AUTOMATIC ACCESS TO ANY NATURE RESERVE, CONSERVATION AREA, WILDERNESS AREA AND / OR STATE FOREST. ANY OTHER / FURTHER CONDITIONS OR RESTRICTIONS THAT THE MANAGER MAY STIPULATE AT HIS / HER DISCRETION MUST ALSO BE ADHERED TO. THIS PERMIT MUST BE AVAILABLE TO BE SHOWN ON DEMAND.
2. The owner of any other land concerned (be it privately or publicly owned land) must give WRITTEN consent allowing the permit holder to enter said property to collect flora / fauna. This written permission must reflect the full name and address of the property owner (or of the person authorised to grant such permission), the full name and address of the person to whom the permission is granted and the number and species of the flora / fauna, the date or dates on which such flora / fauna may be picked / collected and the land in respect of which permission is granted. Copies of this written permission must be made available to The Western Cape Nature Conservation Board upon request.
3. Type-specimens of any newly described / discovered species or other taxon collected must be lodged with a recognised South African scientific institution / museum / herbarium (preferably within the Province of Western Cape) where such material will be available to other researchers. For every flora specimen collected on a Western Cape Nature Conservation Board nature reserve, one additional (extra) herbarium specimen must be forwarded to the Western Cape Nature Conservation Board Herbarium at Jonkershoek (c/o MJ Simpson, Private Bag X5014, Stellenbosch 7599).
4. A list of all collected specimens / material including the; species name, the number collected, the collection date and the precise locality of the collection must be submitted within 14 days from the date of expiry of your permit to The Chief Executive Officer: CapeNature, Private Bag X29, Rondebosch, 7701
5. The maximum number of specimens per species specified in the permit (if at all) may not be exceeded without the prior permission of The Chief Executive Officer: Western Cape Nature Conservation Board.
6. For projects of more than one year's duration a progress report must be submitted to The Chief Executive Officer: Western Cape Nature Conservation Board before 31 December of each year.
7. One copy of all completed reports, publications, or articles (including books, videos, CDs, DVDs etc.) resulting from the project/collection must be submitted to The Chief Executive Officer: Western Cape Nature Conservation Board free of charge.
8. Should a report, publication, article or thesis arise from this project/collection, an acknowledgement to Western Cape Nature Conservation Board must be included.
9. The Forest Act 1984 (Act 122 of 1984) and regulations, the Nature Conservation Ordinance, 1974 (Ordinance 19 of 1974) and all regulations in terms of the Ordinance must be adhered to.
10. Should it be envisaged to export any material / specimens across the boundaries of the Western Cape Province, an export permit will be required in respect of certain species and a further application form will have to be completed. The permit holder must confirm with the Western Cape Nature Conservation Board whether an export permit is required BEFORE exporting any material / specimens from the Western Cape Province.
11. No species that appear on the Red Data List or species listed as endangered in terms of the Nature Conservation Ordinance, 1974 (Ordinance 19 of 1974) may be collected, except for those mentioned on the permit.
12. Unless otherwise specifically indicated in writing, no material or specimens collected with this permit or material or specimens bred or propagated, from material or specimens collected with this permit, may be donated, sold or used for any commercial purpose by any party.
13. I -PPLICABLE, ETHICS CLEARANCE MUST BE ACQUIRED FROM YOUR RESEARCH INSTITUTE PRIOR TO COLLECTION.

Signature Removed
XECUTIVE OFFICER

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APPENDIX 2

Each location with environmental variables used in analysis (Raindays = raindays per annum; MAP = mean annual precipitation; MAT = Mean annual temperature; RH = Relative humidity; MASMS = Mean annual Soil moisture stress; MAPE = Mean annual Potential Evapotranspiration; SAI = Ratio of Actual evapotranspiration to potential evapotranspiration; SAI = sum of the mean precipitation of the four hottest months of the year (Dec - Mar); WCR= % MAP that falls during the winter months April to September); WD = PET (potential evapotranspiration) – MAP (mean annual precipitation); MI = mean annual precipitation divided by the mean annual potential evapotranspiration

Biome	Bioregion	Locality	MAP	MAT	MASMS	MAPE	RH	SAI	WCR	WD	MI
Albany Thicket	Albany Thicket	Addo national Park	431	**17.2**	0.77	**2025**	76.3	143.8	**26%**	1594	0.23
		Graaff Reinet	431	**17.2**	0.77	**2025**	80.7	143.8	**26%**	1594	0.21
Forest	Afromontane forest	Garden route National Park	863	**16.7**		**1647**	73.8	209.8	**40%**	784	0.23
Fynbos	East Coast Renosterveld	Bonnievale	389	**16.4**	0.72	**1948**	75.5	9.2	**72%**	1559	0.22
		Laaiplaas, Robertson	389	**16.4**	0.72	**1948**	75.5	9.2	**72%**	1559	0.22
		Robertson	389	**16.4**	0.72	**1948**	75.5	9.2	**72%**	1559	0.22
		Vrolikheid Nature reserve	389	**16.4**	0.72	**1948**	75.5	9.2	**72%**	1559	0.22
	Karoo Renosterveld	Jagtpan, Karoo	291	**14.4**	0.77	**2417**	51.8	84.2	**33%**	2126	0.28
	Northwest Fynbos	Boesmansberg	403	**15.7**	0.73	**2225**	75.5	9.2	**72%**	1822	0.21
		Cederberg	403	**15.7**	0.73	**2225**	79.1	16.2	**84%**	1822	0.20
		Clanwilliam	403	**15.7**	0.73	**2225**	79.1	16.2	**84%**	1822	0.20
		Grootkloof, clanwilliam	403	**15.7**	0.73	**2225**	79.1	16.2	**84%**	1822	0.20
		Kruisfontein, Elands Bay	403	**15.7**	0.73	**2225**	83.3	27	**86%**	1822	0.19
		Leipoldville	403	**15.7**	0.73	**2225**	83.3	27	**86%**	1822	0.19
		Redelinghuis	403	**15.7**	0.73	**2225**	79.1	16.2	**84%**	1822	0.20
		Sandvlakte	403	**15.7**	0.73	**2225**	75.5	9.2	**72%**	1822	0.21
		Sevilla, Cederberg	403	**15.7**	0.73	**2225**	79.1	16.2	**84%**	1822	0.20
	South Coast Fynbos	Blombos	453	**16.1**	0.71	**1800**	73.8	84.6	**64%**	1347	0.22
		Windhoek Bredasdorp	453	**16.1**	0.71	**1800**	63.3	84.6	**64%**	1347	0.25
	South Strandveld	Byneskranskop, Die kelders	536	**16.6**	0.69	**1756**	75.5	9.2	**72%**	1220	0.22
	Southern Fynbos	Bontebok National Park	598	**15.1**	0.70	**1803**	75.5	9.2	**72%**	1205	0.20
		Grootvadersbosch	598	**15.1**	0.70	**1803**	75.5	9.2	**72%**	1205	0.20
		South Western Cape	598	**15.1**	0.7	**1803**	75.5	9.2	**72%**	1205	0.20
		Swellendam	598	**15.1**	0.70	**1803**	75.5	9.2	**72%**	1205	0.20
	Southwest Fynbos	Caledon	695	**15.7**	0.64	**1892**	75.5	9.2	**72%**	1197	0.21
		Cape Point nature reserve	695	**15.7**	0.64	**1892**	75.5	79.2	**71%**	1197	0.21
		Du toits kloof	695	**15.7**	0.64	**1892**	75.5	9.2	**72%**	1197	0.21
		Voelvlei Dam, Gouda - Tulbagh	695	**15.7**	0.64	**1892**	63.3	21.6	**30%**	1197	0.25
	West Coast Renosterveld	Ikwa ttu	444	**17**	0.70	**2230**	83.3	27	**86%**	1786	0.20
		Piketberg	444	**17**	0.70	**2230**	79.1	16.2	**84%**	1786	0.21
		Riebeekasteel	444	**17**	0.70	**2230**	79.1	16.2	**84%**	1786	0.21
	West Strandveld	Elands Bay	309	**16.5**	0.75	**2202**	83.3	27	**86%**	1893	0.20

		Elandsfontein	309	**16.5**	0.75	**2202**	83.3	27	**86%**	1893	0.20
		Koeberg Nature reserve	309	**16.5**	0.75	**2202**	83.3	27	**86%**	1893	0.20
		West Coast National Park	309	**16.5**	0.75	**2202**	75.5	9.2	**72%**	1893	0.22
		Ysterfontein	309	**16.5**	0.75	**2202**	83.3	27	**86%**	1893	0.20
	Western Fynbos-Renoste	Minwater, oudsthoorn	376	**14.7**	0.76	**2141**	51.8	84.2	**33%**	1765	0.28
		Reiersvlei	376	**14.7**	0.76	**2141**	63.3	21.6	**30%**	1765	0.23
		Witpoortdam area, Swartberg	376	**14.7**	0.76	**2141**	75.5	9.2	**72%**	1765	0.19
	Eastern Fynbos-Rhenost	The Crags, Plettenberg Bay	863	**16.7**		**1647**	73.8	209.8	**40%**	784	0.23
		George and Knysna	863	**16.7**		**1647**	73.8	209.8	**40%**	784	0.23
Nama Karoo	Bushmanland	Augrabies National Park	137	**17.3**	0.86	**2758**	51.8		**7%**	2621	0.33
	Lower Karoo	Karoo National Park	203	**16.4**	0.83	**2435**	63.3	21.6	**30%**	2232	0.26
		Victoria West, Libanon	203	**16.4**	0.83	**2435**	63.3	21.6	**30%**	2232	0.26
	Upper Karoo	Richmond	266	**15.4**	0.83	**2484**	63.3	21.6	**30%**	2218	0.24
Savanna	Kalahari Duneveld	Kgalagadi National Park	184	**18.7**	0.86	**2919**	47.4	204	**1%**	2735	0.39
Succulent Karoo	Knersvlakte	Knersvlakte	132	**18.2**	0.81	**2625**	49	49.8	**76%**	2493	0.37
	Namaqualand Hardeveld	Namaqua National Park	150	**16.7**	0.81	**2544**	49	49.8	**76%**	2394	0.34
		Kamieskroon	150	**16.7**	0.81	**2544**	49	49.8	**76%**	2394	0.34
	Namaqualand Sandveld	Strandfontein	105	**17.6**	0.81	**2558**	83.3	27	**86%**	2453	0.21
	Rainshadow Valley Karoo	Anysberg	209	**16.6**	0.80	**2414**	63.3	21.6	**30%**	2205	0.26
		Botterkloof, Doornbos	209	**16.6**	0.80	**2414**	63.3	21.6	**30%**	2205	0.26
		Laingsburg	209	**16.6**	0.80	**2414**	63.3	21.6	**30%**	2205	0.26
		Montague Baths	209	**16.6**	0.80	**2414**	75.5	9.2	**72%**	2205	0.22
		Willowmore	209	**16.6**	0.80	**2414**	63.3	21.6	**30%**	2205	0.26

2013 data 2013 data

APPENDIX 3

Correlation (Spearman's rho) of meteorological factors for all localities

		MAP	MAT	MASMS	MAPE	RH	SAI	WCR	WD	MI
MAP	Correlation Coefficient	1	-.380**	-.894**	-.835**	.333*	-0.105	0.058	-.953**	.986**
	Sig. (2-tailed)		0.005	0	0	0.014	0.451	0.679	0	0
	N	54	54	53	54	54	54	54	54	54
MAT	Correlation Coefficient		1	.382**	.343*	-0.01	.464**	-0.09	.424**	-.374**
	Sig. (2-tailed)			0.005	0.011	0.944	0	0.519	0.001	0.005
	N		54	53	54	54	54	54	54	54
MASMS	Correlation Coefficient			1	.761**	-.377**	.342*	-.354**	.868**	-.887**
	Sig. (2-tailed)				0	0.005	0.012	0.009	0	0
	N			53	53	53	53	53	53	53
MAPE	Correlation Coefficient				1	-0.216	0.076	0.007	.919**	-.881**
	Sig. (2-tailed)					0.117	0.584	0.959	0	0
	N				54	54	54	54	54	54
RH	Correlation Coefficient					1	-0.142	.623**	-0.23	.305*
	Sig. (2-tailed)						0.306	0	0.095	0.025
	N					54	54	54	54	54
SAI	Correlation Coefficient						1	-.343*	0.156	-0.134
	Sig. (2-tailed)							0.011	0.259	0.335
	N						54	54	54	54
WCR	Correlation Coefficient							1	0.01	0.023
	Sig. (2-tailed)								0.945	0.868
	N							54	54	54
WD	Correlation Coefficient								1	-.981**
	Sig. (2-tailed)									0
	N								54	54

**. Correlation is significant at the 0.01 level (2-tailed).
*. Correlation is significant at the 0.05 level (2-tailed).

MAP	Mean annual precipitation
MAT	Mean annual temperature
MASMS	Mean annual soil moisture stress
MAPE	Mean annual potential evapotranspiration
RH	Relative humidity
SAI	Summer aridity index
WCR	Winter concentration of rainfall
WD	Water deficit

APPENDIX 4

Appendix 4a: Mean values and standard deviations of repeated measurements of standards for inorganic apatite analyses, per run.

Run	Values	CM *	NBS 18	NBS 19	Values	CM *	NBS 18	NBS 19
1	$\delta^{13}C$	0.15	-5	2.09	$\delta^{18}O$	-8.77	-23.06	-2.26
	StdDev	0.07	0.14	0.07	StdDev	0.2	0.14	0.12
2	$\delta^{13}C$	0.04	-4.96	1.94	$\delta^{18}O$	-8.76	-23.09	-2.33
	StdDev	0.19	0.3	0.46	StdDev	0.13	0.18	0.19
3	$\delta^{13}C$	0.3	-5.04	2.04	$\delta^{18}O$	-8.72	-23.1	-2.36
	StdDev	0.11	0.16	0.07	StdDev	0.06	0.21	0.13
4	$\delta^{13}C$	0.3	-5.04	1.98	$\delta^{18}O$	-8.81	-23.07	-2.3
	StdDev	0.18	0.09	0.1	StdDev	0.13	0.26	0.15
5	$\delta^{13}C$	0.26	-5.03	2.01	$\delta^{18}O$	-8.83	-23.07	-2.28
	StdDev	0.14	0.06	0.04	StdDev	0.07	0.08	0.13
6	$\delta^{13}C$	0.29	-5.04	1.99	$\delta^{18}O$	-8.78	-23.08	-2.32
	StdDev	0.12	0.06	0.11	StdDev	0.05	0.07	0.16
7	$\delta^{13}C$	0.28	-5.04	2	$\delta^{18}O$	-8.8	-23.08	-2.31
	StdDev	0.1	0.12	0.05	StdDev	0.06	0.12	0.11
8	$\delta^{13}C$	0.29	-5.04	1.99	$\delta^{18}O$	-8.74	-23.1	-2.35
	StdDev	0.13	0.13	0.07	StdDev	0.05	0.15	0.14
9	$\delta^{13}C$	0.38	-5.06	1.92	$\delta^{18}O$	-8.71	-23.1	-2.37
	StdDev	0.1	0.07	0.07	StdDev	0.16	0.13	0.09
10	$\delta^{13}C$	0.31	-5.04	1.97	$\delta^{18}O$	-8.85	-23.06	-2.27
	StdDev	0.03	0.14	0.13	StdDev	0.04	0.06	0.13
11	$\delta^{13}C$	0.35	-5.05	1.94	$\delta^{18}O$	-8.8	-23.08	-2.3
	StdDev	0.08	0.07	0.07	StdDev	0.04	0.06	0.12
12	$\delta^{13}C$	0.22	-5.02	2.04	$\delta^{18}O$	-8.79	-23.08	-2.31
	StdDev	0.07	0.12	0.09	StdDev	0.03	0.11	0.06
13	$\delta^{13}C$	0.27	-5.03	2	$\delta^{18}O$	-8.89	-23.08	-2.15
	StdDev	0.1	0.11	0.07	StdDev	0.14	0.14	0.15
14	$\delta^{13}C$	0.24	-4.91	1.92	$\delta^{18}O$	-8.9	-22.91	-2.24
	StdDev	0.17	0.22	0.15	StdDev	0.08	0.25	0.25
15	$\delta^{13}C$	0.32	-5.05	1.96	$\delta^{18}O$	-8.79	-23.08	-2.31
	StdDev	0.08	0.11	0.1	StdDev	0.08	0.16	0.26
16	$\delta^{13}C$	0.28	-5.04	1.99	$\delta^{18}O$	-8.96	-23.03	-2.49
	StdDev	0.08	0.17	0.08	StdDev	0.19	0.12	0.6
17	$\delta^{13}C$	0.29	-5.04	1.99	$\delta^{18}O$	-8.86	-23.06	-2.26
	StdDev	0.08	0.2	0.08	StdDev	0.21	0.12	0.1
18	$\delta^{13}C$	0.36	-4.99	1.97	$\delta^{18}O$	-8.78	-23.08	-2.32
	StdDev	0.09	0.12	0.04	StdDev	0.06	0.06	0.11
19	$\delta^{13}C$	0.29	-5.08	2	$\delta^{18}O$	-8.78	-23.08	-2.31
	StdDev	0.13	0.09	0.11	StdDev	0.06	0.04	0.14

* Cavendish Marble

Appendix 4b: Mean values and standard deviations of repeated measurements of for organic bone collagen analyses, per run.

Run	Values	MG **	SEAL	VALINE	Values	MG **	SEAL	VALINE
1	$\delta^{15}N$	7.48	15.81	12.19	$\delta^{13}C$	-20.31	-11.86	-26.65
	StdDev	0.04	0.11	0.11	StdDev	0.08	0.06	0.03
2	$\delta^{15}N$	7.48	15.82	12.18	$\delta^{13}C$	-20.28	-11.87	-26.67
	StdDev	0.06	0.07	0.07	StdDev	0.06	0.09	0.11
3	$\delta^{15}N$	7.49	15.83	12.17	$\delta^{13}C$	-20.26	-11.88	-26.68
	StdDev	0.08	0.05	0.05	StdDev	0.09	0.1	0.08
4	$\delta^{15}N$	7.47	15.8	12.2	$\delta^{13}C$	-20.29	-11.87	-26.67
	StdDev	0.03	0.02	0.06	StdDev	0.06	0.05	0.05
5	$\delta^{15}N$	7.46	15.79	12.23	$\delta^{13}C$	-20.32	-11.85	-26.65
	StdDev	0.03	0.06	0.04	StdDev	0.07	0.03	0.05
6	$\delta^{15}N$	7.47	15.79	12.22	$\delta^{13}C$	-20.31	-11.86	-26.65
	StdDev	0.04	0.04	0.09	StdDev	0.06	0.05	0.04
7	$\delta^{15}N$	7.46	15.79	12.23	$\delta^{13}C$	-20.26	-11.88	-26.68
	StdDev	0.05	0.07	0.08	StdDev	0.12	0.04	0.09
8	$\delta^{15}N$	7.53	15.85	12.25	$\delta^{13}C$	-20.3	-11.86	-26.66
	StdDev	0.09	0.06	0.09	StdDev	0.05	0.1	0.05
9	$\delta^{15}N$	7.49	15.81	12.2	$\delta^{13}C$	-20.29	-11.87	-26.67
	StdDev	0.06	0.05	0.04	StdDev	0.04	0.03	0.06
10	$\delta^{15}N$	7.46	15.78	12.24	$\delta^{13}C$	-20.32	-11.86	-26.65
	StdDev	0.09	0.14	0.08	StdDev	0.06	0.05	0.05
11	$\delta^{15}N$	7.46	15.78	12.24	$\delta^{13}C$	-20.32	-11.86	-26.65
	StdDev	0.09	0.14	0.08	StdDev	0.06	0.05	0.05
12	$\delta^{15}N$	7.47	15.79	12.22	$\delta^{13}C$	-20.24	-11.86	-26.7
	StdDev	0.03	0.04	0.08	StdDev	0.08	0.11	0.04
13	$\delta^{15}N$	7.48	15.81	12.19	$\delta^{13}C$	-20.33	-11.85	-26.64
	StdDev	0.02	0.02	0.05	StdDev	0.12	0.09	0.06
14	$\delta^{15}N$	7.48	15.81	12.2	$\delta^{13}C$	-20.05	-11.97	-26.32
	StdDev	0.08	0.04	0.07	StdDev	0.12	0.09	0.08

** Merck gel

APPENDIX 5

Collagen yields, C: N ratios , %C/%N

UCT specimen number	Wt (mg)	%N	Std corrected $\delta^{15}N$	%C	Std corrected $\delta^{13}C$	C:N ratio elemental	Collagen yield
880	0.493	15.7	14.0	43.0	-20.1	3.2	6%
880	0.461	13.6	14.0	37.3	-20.3	3.2	6%
1074	0.499	15.7	11.5	43.1	-19.3	3.2	26%
1074	0.581	16.0	10.8	43.9	-19.4	3.2	26%
1077	0.517	16.0	14.0	44.0	-18.1	3.2	19%
1077	0.463	15.7	13.8	43.2	-18.8	3.2	19%
1667	0.506	15.3	4.4	42.4	-22.4	3.2	28%
1667	0.499	15.4	4.2	42.6	-22.5	3.2	28%
1670	0.516	15.5	7.9	42.8	-20.3	3.2	24%
1670	0.482	15.9	7.9	43.7	-20.5	3.2	24%
1702	0.498	15.7	12.2	42.9	-14.0	3.2	26%
1702	0.449	15.7	12.1	43.0	-13.8	3.2	26%
1708	0.46	16.4	9.5	44.8	-17.5	3.2	28%
1708	0.492	16.1	9.2	43.8	-17.7	3.2	28%
1709	0.453	15.5	12.9	42.2	-17.1	3.2	27%
1709	0.475	16.2	12.8	43.9	-16.7	3.2	27%
1710	0.49	15.7	12.7	44.4	-16.6	3.3	29%
1710	0.576	15.6	12.3	43.5	-16.5	3.2	29%
1711	0.551	15.6	12.5	44.5	-16.6	3.3	29%
1711	0.494	15.6	12.3	44.1	-16.6	3.3	29%
1716	0.518	15.3	14.7	43.8	-17.3	3.3	25%
1717	0.534	12.8	11.8	36.1	-18.4	3.3	22%
1717	0.488	15.3	11.7	43.1	-18.4	3.3	22%
1718	0.536	19.3	11.2	53.8	-13.0	3.3	22%
1718	0.497	15.5	11.3	43.1	-13.2	3.2	22%
1719	0.5	15.9	7.2	43.9	-19.1	3.2	26%
1719	0.53	15.7	7.4	43.3	-19.2	3.2	26%
1720	0.486	16.1	11.5	44.7	-18.2	3.2	23%
1720	0.516	15.7	11.6	43.0	-18.0	3.2	23%
2061	0.459	14.4	10.7	43.1	-15.1	3.5	22%
2061	0.563	14.1	10.8	42.2	-15.2	3.5	22%
2063	0.56	15.4	5.4	42.5	-20.6	3.2	26%
2063	0.468	15.7	5.4	43.0	-20.9	3.2	26%
2066	0.461	15.4	14.1	42.0	-20.2	3.2	25%
2066	0.467	18.4	14.1	50.0	-20.1	3.2	25%
2067	0.508	15.7	13.3	43.5	-20.0	3.2	18%
2067	0.455	15.5	13.2	42.4	-20.2	3.2	18%
2073	0.517	15.7	7.2	43.3	-19.8	3.2	24%
2073	0.456	16.2	7.2	44.3	-19.9	3.2	24%
2080	0.483	16.7	5.4	46.5	-22.0	3.3	28%
2080	0.505	15.6	5.5	43.3	-21.5	3.2	28%
2111	0.486	15.7	5.6	43.7	-21.1	3.2	26%
2111	0.485	15.2	5.5	42.0	-21.2	3.2	26%
2130	0.527	16.1	13.1	44.4	-17.3	3.2	26%
2130	0.454	15.8	12.8	43.5	-17.3	3.2	26%
2274	0.507	15.4	8.7	43.4	-20.9	3.3	20%
2274	0.47	15.5	8.6	42.8	-21.0	3.2	20%
2637	0.554	16.1	12.2	44.4	-13.8	3.2	20%
2637	0.519	15.8	12.4	43.5	-14.7	3.2	20%
2637	0.532	15.7	12.2	43.2	-14.0	3.2	20%
2638	0.558	15.6	13.6	43.5	-15.8	3.3	25%
2638	0.512	15.2	13.4	42.4	-16.2	3.3	25%
2640	0.527	15.8	12.0	43.7	-12.6	3.2	22%

APPENDIX 5

Collagen yields, C: N ratios , %C/%N

UCT specimen number	Wt (mg)	%N	Std corrected $\delta^{15}N$	%C	Std corrected $\delta^{13}C$	C:N ratio elemental	Collagen yield
2640	0.466	15.4	11.9	42.4	-13.0	3.2	22%
2641	0.454	16.4	12.4	45.4	-13.9	3.2	24%
2641	0.471	15.9	12.4	43.7	-13.6	3.2	24%
2643	0.523	15.8	12.4	43.2	-13.6	3.2	23%
2643	0.535	13.8	12.5	37.8	-14.1	3.2	23%
2645	0.509	15.5	12.2	42.6	-13.4	3.2	27%
2645	0.528	12.9	12.5	35.3	-13.0	3.2	27%
2646	0.5	12.2	12.2	33.6	-13.8	3.2	22%
2646	0.497	15.7	12.4	43.2	-14.0	3.2	22%
2647	0.523	15.8	12.5	43.0	-13.2	3.2	24%
2647	0.519	16.3	12.4	44.3	-13.0	3.2	24%
2648	0.544	15.1	11.7	41.8	-14.2	3.2	34%
2648	0.468	15.5	11.8	42.7	-13.9	3.2	34%
2649	0.495	15.8	10.5	43.4	-12.6	3.2	25%
2649	0.466	14.2	10.3	38.7	-11.8	3.2	25%
2650	0.509	14.3	13.0	40.1	-15.2	3.3	20%
2650	0.47	15.7	12.9	43.3	-14.0	3.2	20%
2651	0.536	13.4	12.9	36.6	-12.4	3.2	21%
2651	0.464	13.3	12.1	36.4	-12.2	3.2	21%
2659	0.458	15.9	8.7	44.2	-18.1	3.2	25%
2659	0.483	15.8	8.7	43.4	-18.1	3.2	25%
2660	0.486	14.8	10.4	40.8	-17.0	3.2	21%
2660	0.489	15.6	9.9	42.7	-17.5	3.2	21%
3933	0.492	19.5	10.0	54.7	-18.7	3.3	6%
3933	0.51	15.7	10.1	43.9	-18.9	3.3	6%
4082	0.486	14.6	6.2	40.4	-19.1	3.2	20%
4082	0.55	14.2	6.1	39.0	-19.4	3.2	20%
4290	0.495	14.3	14.1	39.5	-14.8	3.2	22%
4290	0.488	15.3	14.1	42.2	-14.7	3.2	22%
7732	0.487	15.8	11.4	43.2	-8.6	3.2	17%
7732	0.508	12.4	11.4	33.8	-8.7	3.2	17%
7733	0.501	15.5	11.4	42.4	-9.3	3.2	24%
7733	0.469	15.7	11.5	42.8	-9.3	3.2	24%
7734	0.471	15.9	11.9	45.2	-8.3	3.3	18%
7734	0.475	15.5	11.7	43.2	-7.8	3.3	18%
7735	0.51	16.0	13.8	44.8	-15.2	3.3	20%
7735	0.495	15.5	13.7	43.2	-15.4	3.3	20%
7736	0.526	16.2	13.3	44.4	-12.8	3.2	16%
7736	0.521	15.9	13.1	43.6	-12.9	3.2	16%
7737	0.576	16.3	14.3	45.6	-10.7	3.3	23%
7737	0.523	15.6	14.4	43.4	-10.5	3.3	23%
7738	0.519	15.6	14.4	43.4	-11.1	3.2	26%
7738	0.525	16.2	14.6	44.6	-11.1	3.2	26%
7739	0.51	16.3	15.1	44.8	-11.0	3.2	24%
7739	0.583	15.7	15.1	43.1	-10.7	3.2	24%
7740	0.456	16.2	14.1	44.7	-12.3	3.2	25%
7740	0.465	16.5	14.0	45.4	-12.2	3.2	25%
7741	0.497	15.5	14.4	43.2	-12.8	3.3	11%
7741	0.497	16.0	14.4	44.2	-12.9	3.2	11%
7742	0.464	16.6	12.8	46.1	-13.2	3.2	18%
7742	0.482	14.9	12.7	41.3	-13.4	3.2	18%
7749	0.46	15.4	11.7	42.2	-15.0	3.2	23%
7749	0.498	16.0	11.9	43.8	-15.6	3.2	23%

APPENDIX 5

Collagen yields, C: N ratios , %C/%N

UCT specimen number	Wt (mg)	%N	Std corrected $\delta^{15}N$	%C	Std corrected $\delta^{13}C$	C:N ratio elemental	Collagen yield
7774	0.472	15.8	11.1	43.6	-8.6	3.2	27%
7774	0.501	14.7	11.7	40.5	-8.5	3.2	27%
7776	0.475	18.4	11.8	51.1	-12.1	3.2	21%
7776	0.518	15.7	11.7	43.0	-11.8	3.2	21%
7782	0.469	15.6	9.2	43.1	-19.1	3.2	25%
7782	0.473	15.7	9.4	43.3	-19.1	3.2	25%
8080	0.486	15.6	11.9	43.1	-19.9	3.2	27%
8080	0.485	11.4	11.9	31.0	-20.0	3.2	27%
8082	0.461	15.9	12.8	45.1	-19.9	3.3	27%
8082	0.554	15.7	13.2	44.1	-20.0	3.3	27%
8085	0.569	14.7	12.3	42.8	-20.1	3.4	30%
8085	0.451	15.6	12.8	43.5	-20.0	3.3	30%
8086	0.551	15.8	11.7	45.5	-20.5	3.4	30%
8086	0.479	15.6	11.8	44.1	-20.5	3.3	30%
8090	0.53	15.1	11.2	46.9	-20.6	3.6	32%
8098	0.516	16.8	12.0	46.4	-18.9	3.2	26%
8098	0.498	15.5	11.9	42.7	-19.0	3.2	26%
8104	0.489	15.1	11.4	44.3	-19.6	3.4	29%
8104	0.53	16.2	11.6	45.4	-19.1	3.3	29%
8106	0.477	15.1	12.1	44.4	-20.8	3.4	26%
8106	0.579	15.2	12.3	44.5	-20.7	3.4	26%
13954	0.433	15.1	5.9	41.4	-20.3	3.2	22%
13954	0.468	15.9	5.8	43.2	-19.6	3.2	22%
13955	0.49	14.9	11.4	40.9	-22.0	3.2	25%
13955	0.517	16.5	10.7	45.1	-21.9	3.2	25%
13956	0.446	15.7	5.6	44.2	-20.3	3.3	21%
13956	0.557	15.0	5.6	41.6	-18.9	3.2	21%
13957	0.582	14.7	6.1	42.0	-19.8	3.3	25%
13957	0.446	15.8	5.8	44.7	-20.3	3.3	25%
13958	0.401	15.4	3.6	42.7	-22.2	3.2	23%
13958	0.512	15.2	3.5	41.9	-22.2	3.2	23%
13959	0.458	12.9	9.6	35.8	-22.8	3.3	20%
13959	0.559	14.8	9.5	40.9	-22.7	3.2	20%
13960	0.479	15.8	8.0	43.3	-16.8	3.2	22%
13960	0.446	16.1	7.7	43.7	-17.2	3.2	22%
13961	0.5	14.1	4.7	39.0	-20.6	3.2	23%
13961	0.43	15.6	4.5	42.5	-20.6	3.2	23%
13962	0.459	15.7	5.6	42.9	-9.9	3.2	24%
13962	0.401	15.2	5.6	41.5	-10.5	3.2	24%
13963	0.518	15.1	6.3	41.4	-19.0	3.2	20%
13963	0.432	16.2	6.5	44.2	-18.8	3.2	20%
13966	0.509	14.0	5.2	38.9	-19.1	3.3	23%
13966	0.53	13.8	5.0	38.2	-18.9	3.2	23%
13970	0.568	16.1	8.1	44.5	-14.5	3.2	20%
13970	0.589	15.2	8.1	41.6	-13.7	3.2	20%
13971	0.458	14.5	7.4	40.0	-21.8	3.2	27%
13971	0.559	16.0	7.5	43.6	-21.7	3.2	27%
13972	0.582	15.3	7.9	43.6	-22.1	3.3	26%
13972	0.489	14.0	7.1	39.0	-22.2	3.2	26%
13973	0.466	15.2	3.8	42.1	-21.3	3.2	23%
13973	0.376	15.5	4.0	42.9	-21.2	3.2	23%
13974	0.457	15.5	4.2	42.5	-21.3	3.2	25%
13974	0.495	15.7	4.5	43.0	-21.5	3.2	25%

APPENDIX 5

Collagen yields, C: N ratios , %C/%N

UCT specimen number	Wt (mg)	%N	Std corrected $\delta^{15}N$	%C	Std corrected $\delta^{13}C$	C:N ratio elemental	Collagen yield
13976	0.525	15.9	17.4	43.7	-17.4	3.2	21%
13976	0.469	16.0	17.9	43.9	-17.7	3.2	21%
13977	0.38	16.0	2.0	43.6	-20.8	3.2	28%
13977	0.533	2.4	1.6	6.5	-21.0	3.2	28%
13978	0.49	15.7	16.2	43.0	-21.1	3.2	25%
13978	0.507	14.8	16.0	40.4	-21.4	3.2	25%
13979	0.506	15.9	10.0	44.0	-19.9	3.2	30%
13979	0.532	13.7	10.0	37.6	-19.9	3.2	30%
13980	0.474	14.7	7.8	41.1	-20.1	3.3	26%
13980	0.485	15.4	7.6	42.6	-19.5	3.2	26%
13981	0.508	14.8	11.3	41.4	-19.1	3.3	22%
13981	0.414	15.4	11.3	43.3	-19.1	3.3	22%
13982	0.518	15.3	7.7	42.5	-20.0	3.2	29%
13982	0.538	15.4	7.8	42.5	-20.1	3.2	29%
13983	0.445	15.3	7.3	42.1	-20.5	3.2	26%
13983	0.461	15.9	8.1	43.3	-19.9	3.2	26%
13984	0.459	15.7	4.6	43.1	-19.8	3.2	21%
13984	0.477	15.3	4.5	41.8	-20.0	3.2	21%
13985	0.497	13.8	10.5	37.8	-18.5	3.2	23%
13985	0.482	16.6	10.4	45.4	-18.6	3.2	23%
13986	0.587	15.2	8.7	42.2	-19.6	3.2	25%
13986	0.525	15.1	8.4	41.5	-19.7	3.2	25%
13986	0.445	16.1	7.5	43.9	-20.7	3.2	25%
13986	0.46	14.7	7.1	39.9	-20.6	3.2	25%
13988	0.469	15.6	5.3	42.8	-19.9	3.2	24%
13988	0.488	15.9	5.1	43.5	-19.8	3.2	24%
13989	0.487	14.7	5.1	40.9	-20.8	3.2	26%
13989	0.482	15.3	5.3	42.2	-19.7	3.2	26%
13990	0.475	15.1	10.6	41.5	-18.6	3.2	13%
13990	0.414	15.4	10.7	42.1	-18.4	3.2	13%
13991	0.441	15.4	7.7	42.9	-19.4	3.2	29%
13991	0.507	16.0	7.6	44.0	-19.7	3.2	29%
13992	0.471	13.8	7.2	38.7	-20.4	3.3	25%
13992	0.495	15.9	7.9	44.3	-20.1	3.2	25%
13993	0.491	14.8	12.4	41.2	-15.5	3.2	25%
13993	0.418	15.3	11.7	42.4	-15.7	3.2	25%
13994	0.39	15.3	5.6	43.4	-20.0	3.3	23%
13994	0.46	15.7	5.2	43.4	-18.9	3.2	23%
13995	0.471	15.4	16.0	42.5	-19.2	3.2	23%
13995	0.469	15.3	9.4	42.0	-19.8	3.2	23%
13995	0.471	14.9	9.7	40.9	-19.0	3.2	23%
13996	0.509	15.1	11.6	43.3	-23.0	3.4	25%
13996	0.486	14.8	11.5	42.1	-22.9	3.3	25%
13997	0.389	15.4	7.6	43.3	-18.5	3.3	24%
13997	0.463	15.7	7.8	43.5	-18.4	3.2	24%
13998	0.454	15.8	10.7	43.1	-20.2	3.2	28%
13998	0.516	15.5	10.6	42.5	-22.1	3.2	28%
13999	0.468	15.3	10.4	42.0	-16.5	3.2	18%
13999	0.415	15.7	10.8	43.1	-16.8	3.2	18%
14000	0.423	15.1	11.5	43.6	-11.3	3.4	24%
14000	0.507	16.2	11.4	44.4	-11.9	3.2	24%
14000	0.563	13.7	10.3	37.2	-10.6	3.2	24%
14001	0.488	15.7	11.8	43.2	-11.6	3.2	27%

APPENDIX 5

Collagen yields, C: N ratios , %C/%N

UCT specimen number	Wt (mg)	%N	Std corrected $\delta^{15}N$	%C	Std corrected $\delta^{13}C$	C:N ratio elemental	Collagen yield
14001	0.559	15.6	11.9	42.6	-11.6	3.2	27%
14001	0.557	15.4	12.2	42.0	-12.0	3.2	27%
14002	0.458	15.8	12.5	43.6	-12.3	3.2	24%
14002	0.524	15.5	12.3	42.6	-12.2	3.2	24%
14003	0.552	13.4	4.4	40.2	-23.3	3.5	27%
14003	0.452	14.9	4.6	43.5	-23.1	3.4	27%
14005	0.488	15.9	9.8	43.7	-20.1	3.2	23%
14005	0.494	15.6	9.7	42.8	-19.6	3.2	23%
14006	0.458	15.6	5.4	43.7	-20.3	3.3	25%
14006	0.512	14.8	5.6	41.0	-19.6	3.2	25%
14007	0.495	15.5	6.3	43.6	-20.1	3.3	26%
14007	0.429	15.5	5.7	43.4	-20.1	3.3	26%
14008	0.472	15.1	8.4	42.1	-16.3	3.3	25%
14008	0.466	15.3	8.2	42.6	-15.5	3.3	25%
14009	0.522	15.2	4.3	42.1	-21.2	3.2	24%
14009	0.463	15.6	4.4	42.9	-21.1	3.2	24%
14010	0.577	15.4	7.3	42.9	-17.9	3.3	23%
14010	0.467	14.8	7.2	40.8	-18.1	3.2	23%
14011	0.483	15.7	7.5	43.0	-17.7	3.2	22%
14011	0.446	15.6	7.1	42.6	-17.8	3.2	22%
14013	0.481	17.4	11.5	54.0	-16.6	3.6	28%
14013	0.463	14.3	11.9	43.2	-16.3	3.5	28%
14014	0.514	16.0	8.8	45.0	-18.7	3.3	28%
14014	0.496	14.6	8.3	40.7	-18.8	3.2	28%
14016	0.485	14.5	5.6	41.6	-21.4	3.4	24%
14016	0.451	15.6	5.7	43.9	-21.6	3.3	24%
14018	0.549	14.3	6.6	43.9	-22.7	3.6	30%
14018	0.522	14.2	6.7	41.8	-22.6	3.4	30%
14032	0.537	15.6	7.6	42.8	-15.5	3.2	24%
14032	0.538	15.6	7.8	42.7	-14.9	3.2	24%
14033	0.508	15.4	6.9	42.6	-21.6	3.2	23%
14033	0.449	15.9	6.9	43.6	-21.4	3.2	23%
14127	0.485	15.6	9.5	43.7	-20.4	3.3	13%
14127	0.463	15.3	9.9	42.8	-20.5	3.3	13%
14128	0.463	15.9	15.2	43.8	-17.5	3.2	28%
14128	0.583	15.8	15.2	43.3	-17.4	3.2	28%
14129	0.517	15.7	9.8	43.0	-19.0	3.2	27%
14129	0.481	15.8	9.6	43.0	-19.1	3.2	27%
14131	0.471	16.7	9.7	48.7	-19.1	3.4	22%
14131	0.514	15.2	9.1	43.8	-19.1	3.4	22%
14132	0.425	15.4	7.1	42.6	-20.0	3.2	15%
14132	0.469	15.5	6.7	42.7	-20.0	3.2	15%
14134	0.497	15.4	11.2	43.0	-19.8	3.3	31%
14134	0.529	15.8	10.7	43.8	-19.8	3.2	31%
14135	0.512	15.8	10.8	43.5	-20.0	3.2	28%
14135	0.379	15.7	10.1	43.2	-20.2	3.2	28%
14136	0.497	15.2	5.1	41.8	-20.8	3.2	27%
14136	0.505	15.6	5.4	42.7	-20.7	3.2	27%
14220	0.521	14.6	10.0	43.2	-20.8	3.5	28%
14220	0.49	14.9	10.6	43.8	-20.5	3.4	28%
14222	0.494	14.9	10.7	42.9	-12.8	3.4	21%
14222	0.55	15.5	11.7	43.3	-12.1	3.3	21%
14223	0.435	15.0	12.4	43.2	-20.7	3.4	25%

APPENDIX 5

Collagen yields, C: N ratios , %C/%N

UCT specimen number	Wt (mg)	%N	Std corrected $\delta^{15}N$	%C	Std corrected $\delta^{13}C$	C:N ratio elemental	Collagen yield
14225	0.552	14.9	10.2	42.8	-13.2	3.4	21%
14225	0.472	15.3	10.6	43.9	-13.2	3.3	21%
14226	0.445	15.8	10.3	43.2	-9.0	3.2	27%
14226	0.563	15.3	10.0	41.4	-9.2	3.2	27%
14228	0.433	15.0	10.2	42.2	-20.3	3.3	21%
14228	0.453	15.5	10.0	43.2	-20.2	3.3	21%
14230	0.475	14.3	10.0	43.5	-21.3	3.5	21%
14230	0.429	15.5	9.1	44.0	-20.3	3.3	21%
14231	0.558	14.3	10.8	41.4	-12.1	3.4	24%
14231	0.474	16.9	10.7	48.8	-12.2	3.4	24%
14233	0.487	15.0	9.2	43.1	-10.4	3.3	29%
14233	0.486	15.9	9.7	43.4	-10.0	3.2	29%
14234	0.474	15.0	9.4	41.4	-8.9	3.2	28%
14234	0.446	15.5	9.1	42.5	-8.8	3.2	28%
14236	0.495	14.1	12.7	43.1	-20.7	3.6	24%
14236	0.48	15.0	12.6	44.5	-20.6	3.5	24%
14240	0.451	15.3	9.3	43.8	-19.4	3.4	22%
14240	0.46	15.4	9.3	43.8	-19.8	3.3	22%
14241	0.5	14.8	9.8	41.2	-20.6	3.2	30%
14241	0.581	15.7	9.6	43.6	-20.6	3.2	30%
14242	0.568	15.8	10.2	43.6	-19.9	3.2	19%
14242	0.569	15.0	9.4	41.5	-19.6	3.2	19%
14243	0.478	16.1	9.6	45.3	-19.0	3.3	28%
14243	0.484	16.8	9.8	47.0	-19.0	3.3	28%
14243	0.482	15.6	10.4	43.4	-18.9	3.2	28%
14244	0.464	15.3	10.5	42.6	-19.8	3.2	23%
14244	0.534	14.9	10.5	41.2	-19.8	3.2	23%
14245	0.462	14.9	9.6	41.4	-19.9	3.2	25%
14245	0.512	15.7	10.4	43.5	-19.8	3.2	25%
14246	0.487	11.5	10.2	35.0	-21.2	3.5	23%
14246	0.504	15.1	10.7	44.4	-20.9	3.4	23%
14247	0.486	15.4	11.4	42.0	-19.9	3.2	26%
14247	0.475	15.6	11.3	42.5	-20.2	3.2	26%
14248	0.401	15.2	10.7	42.5	-20.0	3.3	21%
14248	0.512	15.6	9.9	43.3	-19.9	3.2	21%
14249	0.446	15.8	10.6	44.0	-19.8	3.3	25%
14249	0.523	15.4	10.5	42.5	-20.1	3.2	25%
14250	0.473	14.5	12.1	40.2	-19.1	3.2	26%
14250	0.541	15.7	11.9	43.0	-19.3	3.2	26%
14251	0.432	15.7	10.4	43.3	-16.7	3.2	25%
14251	0.562	15.4	10.7	42.2	-17.0	3.2	25%
14252	0.5	15.5	10.3	45.1	-17.7	3.4	29%
14252	0.483	15.1	10.2	43.8	-17.4	3.4	29%
14255	0.537	15.1	10.9	44.5	-8.6	3.4	
14256	0.417	14.7	9.2	45.0	-14.3	3.6	15%
14256	0.456	13.7	9.2	41.5	-14.0	3.5	15%
14257	0.515	15.8	10.2	45.7	-12.1	3.4	26%
14257	0.524	15.6	9.9	44.3	-12.2	3.3	26%
14258	0.358	15.2	9.3	44.2	-12.2	3.4	17%
14258	0.424	15.4	9.0	44.7	-12.1	3.4	17%
14259	0.494	15.3	9.9	44.7	-11.7	3.4	24%
14259	0.475	14.8	9.9	42.9	-11.4	3.4	24%
14262	0.463	15.4	9.7	42.9	-9.2	3.3	25%

APPENDIX 5

Collagen yields, C: N ratios , %C/%N

UCT specimen number	Wt (mg)	%N	Std corrected $\delta^{15}N$	%C	Std corrected $\delta^{13}C$	C:N ratio elemental	Collagen yield
14262	0.544	15.7	9.7	43.6	-9.1	3.2	25%
14263	0.497	15.7	12.3	43.7	-9.7	3.3	23%
14263	0.474	15.3	12.3	42.4	-9.9	3.2	23%
14264	0.455	15.7	10.4	43.2	-9.3	3.2	30%
14264	0.426	15.6	10.2	42.8	-9.2	3.2	30%
14265	0.477	14.8	8.9	41.7	-13.2	3.3	25%
14265	0.483	15.5	9.0	43.7	-12.7	3.3	25%
14266	0.481	14.9	9.5	41.8	-17.8	3.3	20%
14266	0.508	15.5	9.2	43.3	-17.8	3.3	20%
14267	0.472	15.2	10.5	43.8	-13.0	3.4	22%
14267	0.512	15.4	10.6	43.7	-12.6	3.3	22%
14268	0.43	15.3	8.9	42.9	-13.4	3.3	23%
14268	0.48	15.5	8.9	43.1	-12.9	3.2	23%
14272	0.532	14.9	8.3	41.2	-14.2	3.2	24%
14272	0.524	15.3	8.1	41.8	-15.6	3.2	24%
14275	0.503	15.5	10.8	44.6	-13.5	3.4	
14285	0.506	15.8	10.7	43.1	-8.3	3.2	21%
14285	0.534	15.3	10.4	41.7	-8.2	3.2	21%
14286	0.462	15.0	11.8	42.1	-12.1	3.3	23%
14286	0.539	14.3	11.9	39.7	-11.7	3.2	23%
14287	0.501	13.6	10.1	38.7	-10.5	3.3	17%
14287	0.485	14.3	10.0	40.5	-10.5	3.3	17%
14288	0.484	15.3	9.0	42.4	-9.2	3.2	25%
14288	0.508	15.5	8.7	42.6	-9.2	3.2	25%
14289	0.473	14.8	12.9	41.0	-13.1	3.2	27%
14289	0.476	15.4	12.9	42.7	-13.4	3.2	27%
14290	0.425	15.6	11.3	43.3	-11.9	3.2	25%
14290	0.579	15.2	11.1	42.0	-11.6	3.2	25%
14290	0.518	14.2	11.1	39.0	-11.8	3.2	25%
14291	0.356	15.0	13.3	41.7	-10.4	3.3	25%
14291	0.51	15.4	13.0	42.7	-10.1	3.2	25%
14292	0.468	14.6	9.5	40.4	-9.6	3.2	24%
14292	0.391	15.5	9.7	42.5	-9.5	3.2	24%
14293	0.569	15.2	12.3	43.0	-19.6	3.3	24%
14293	0.456	14.5	12.1	40.8	-19.8	3.3	24%
14294	0.483	14.5	10.8	41.2	-8.7	3.3	21%
14294	0.497	15.2	10.8	42.8	-8.8	3.3	21%
14295	0.449	15.4	12.2	42.0	-11.7	3.2	23%
14295	0.522	14.9	12.7	40.7	-11.6	3.2	23%
14296	0.415	14.9	12.9	43.0	-10.8	3.4	24%
14296	0.491	14.9	12.5	42.6	-10.9	3.3	24%
14297	0.51	14.9	10.1	42.4	-11.9	3.3	24%
14297	0.48	14.4	10.5	40.8	-13.2	3.3	24%
14298	0.42	14.9	15.6	42.1	-13.9	3.3	26%
14298	0.512	14.3	14.1	40.2	-13.0	3.3	26%
14299	0.426	15.4	15.0	42.4	-14.8	3.2	18%
14299	0.506	15.3	15.4	42.0	-14.8	3.2	18%
14300	0.494	12.5	9.7	35.0	-17.1	3.3	22%
14300	0.533	15.2	9.3	42.0	-17.9	3.2	22%
14301	0.501	15.2	9.3	43.3	-11.8	3.3	20%
14301	0.479	15.4	8.8	43.6	-13.2	3.3	20%
14302	0.498	15.0	11.8	42.8	-12.4	3.3	23%
14302	0.521	15.5	11.6	43.3	-11.6	3.3	23%

APPENDIX 5

Collagen yields, C: N ratios , %C/%N

UCT specimen number	Wt (mg)	%N	Std corrected $\delta^{15}N$	%C	Std corrected $\delta^{13}C$	C:N ratio elemental	Collagen yield
14303	0.465	15.3	10.4	44.3	-10.6	3.4	20%
14303	0.475	15.6	10.3	43.0	-11.2	3.2	20%
14304	0.49	15.7	8.0	42.8	-20.7	3.2	30%
14304	0.368	15.3	8.3	41.4	-21.3	3.2	30%
14305	0.477	14.9	13.5	41.7	-16.3	3.3	26%
14305	0.459	15.6	13.2	42.7	-17.0	3.2	26%
14307	0.46	15.6	15.2	42.6	-18.4	3.2	26%
14307	0.551	15.3	15.5	41.9	-18.4	3.2	26%
14308	0.387	15.3	12.5	42.3	-11.6	3.2	27%
14308	0.462	15.2	12.2	41.7	-12.0	3.2	27%
14309	0.526	14.9	10.3	40.9	-9.1	3.2	28%
14309	0.383	15.4	11.5	42.1	-9.4	3.2	28%
14310	0.518	14.5	11.0	40.7	-9.5	3.3	29%
14310	0.565	15.6	11.0	42.5	-9.0	3.2	29%
14311	0.545	15.3	10.8	42.2	-6.8	3.2	23%
14311	0.491	15.4	10.7	42.4	-7.0	3.2	23%
14312	0.454	15.5	11.9	42.4	-15.4	3.2	25%
14312	0.563	15.5	12.0	42.3	-14.8	3.2	25%
14313	0.498	14.9	10.8	41.0	-7.9	3.2	24%
14313	0.428	15.5	10.6	42.3	-7.9	3.2	24%
14314	0.431	15.1	12.0	41.7	-7.6	3.2	18%
14314	0.471	15.9	12.0	43.6	-7.6	3.2	18%
14315	0.573	15.3	11.8	41.8	-19.6	3.2	29%
14315	0.551	15.6	11.9	42.3	-19.9	3.2	29%
14316	0.524	15.4	10.9	42.1	-8.5	3.2	24%
14316	0.488	15.1	10.6	41.0	-8.3	3.2	24%
14317	0.463	15.5	12.2	42.7	-10.0	3.2	22%
14317	0.44	15.3	12.5	42.1	-9.9	3.2	22%
14318	0.529	23.5	10.7	64.6	-7.7	3.2	24%
14318	0.389	15.3	10.3	42.1	-7.7	3.2	24%
14319	0.461	15.2	12.1	41.5	-8.0	3.2	22%
14319	0.512	15.4	12.3	42.1	-7.9	3.2	22%
14320	0.491	15.1	11.0	41.9	-8.1	3.2	27%
14320	0.494	15.3	11.2	41.8	-7.9	3.2	27%
14321	0.437	15.0	11.1	42.3	-20.7	3.3	22%
14321	0.487	14.7	10.9	41.2	-20.3	3.3	22%
14322	0.471	15.3	11.9	42.1	-19.5	3.2	21%
14322	0.423	15.4	11.2	42.2	-19.4	3.2	21%
14323	0.401	15.8	10.5	44.0	-18.8	3.2	27%
14323	0.516	15.4	10.7	42.7	-19.4	3.2	27%
14324	0.485	15.0	11.9	41.3	-8.1	3.2	28%
14324	0.472	15.5	11.5	42.5	-8.3	3.2	28%
14325	0.488	12.9	11.0	35.2	-8.8	3.2	24%
14325	0.488	12.9	11.0	35.2	-8.8	3.2	24%
14325	0.42	15.1	11.5	41.3	-8.3	3.2	24%
14325	0.559	15.7	11.0	42.9	-8.4	3.2	24%
14325	0.559	15.7	11.0	42.9	-8.4	3.2	24%
14326	0.536	15.4	10.9	42.2	-21.0	3.2	22%
14326	0.353	15.3	11.4	41.6	-21.2	3.2	22%
14352	0.561	15.5	6.2	44.2	-12.1	3.3	29%
14352	0.523	15.1	6.1	42.6	-10.6	3.3	29%
14352	0.496	15.6	6.1	43.7	-11.0	3.3	29%
14353	0.444	14.4	5.9	43.4	-21.2	3.5	22%

APPENDIX 5

Collagen yields, C: N ratios , %C/%N

UCT specimen number	Wt (mg)	%N	Std corrected $\delta^{15}N$	%C	Std corrected $\delta^{13}C$	C:N ratio elemental	Collagen yield
14353	0.512	14.6	5.5	42.8	-20.8	3.4	22%
14354	0.511	14.3	6.8	42.5	-21.4	3.5	24%
14354	0.403	15.1	6.1	42.8	-20.7	3.3	24%
14355	0.474	14.2	6.8	42.4	-13.9	3.5	26%
14355	0.424	15.0	6.0	42.6	-12.7	3.3	26%
14356	0.501	14.2	5.6	43.0	-20.8	3.5	25%
14356	0.495	15.2	5.7	43.0	-21.3	3.3	25%
14357	0.502	14.9	6.0	42.7	-20.7	3.3	30%
14357	0.39	15.2	5.8	42.9	-20.7	3.3	30%
14358	0.57	14.7	6.4	42.8	-11.3	3.4	25%
14358	0.515	18.8	6.6	54.3	-11.9	3.4	25%
14358	0.485	15.0	6.3	43.2	-12.1	3.4	25%
14359	0.467	15.2	6.7	46.2	-13.3	3.5	29%
14359	0.558	14.5	6.2	43.1	-12.6	3.5	29%
14360	0.479	15.1	5.8	43.1	-20.4	3.3	21%
14360	0.525	15.0	6.0	42.8	-20.3	3.3	21%
14361	0.526	14.8	6.1	44.1	-21.0	3.5	32%
14361	0.486	15.1	6.2	45.1	-21.5	3.5	32%
14363	0.567	15.0	5.4	43.2	-20.5	3.4	24%
14363	0.561	14.5	5.2	41.5	-20.7	3.3	24%
14364	0.501	14.9	5.9	43.7	-21.1	3.4	27%
14364	0.434	15.2	5.5	42.6	-20.9	3.3	27%
14365	0.532	14.5	6.2	41.4	-20.6	3.3	24%
14365	0.453	15.1	5.8	42.9	-20.7	3.3	24%
14366	0.501	11.4	7.0	33.2	-20.5	3.4	24%
14366	0.525	15.0	7.1	43.2	-20.3	3.4	24%
14367	0.477	15.6	6.1	43.5	-11.9	3.3	29%
14367	0.501	15.1	5.9	41.8	-11.5	3.2	29%
14368	0.469	15.4	7.2	44.7	-19.9	3.4	22%
14368	0.493	15.0	6.8	43.3	-19.8	3.4	22%
14368	0.58	15.3	6.5	44.1	-19.8	3.4	22%
14369	0.573	15.0	5.6	42.8	-11.0	3.3	26%
14370	0.5	14.4	5.5	41.3	-20.6	3.3	23%
14370	0.551	15.0	5.6	43.1	-20.5	3.3	23%
14371	0.459	14.9	6.3	42.7	-10.8	3.4	25%
14371	0.485	15.0	6.4	42.6	-11.0	3.3	25%
14372	0.464	14.4	5.8	41.7	-21.2	3.4	27%
14372	0.475	15.1	5.3	43.1	-20.3	3.3	27%
14373	0.465	15.1	6.4	44.0	-13.8	3.4	25%
14373	0.487	15.6	6.3	45.3	-14.1	3.4	25%
14373	0.517	15.1	6.3	43.6	-13.6	3.4	25%
14374	0.471	15.8	9.3	43.7	-22.0	3.2	20%
14374	0.47	15.5	9.1	42.5	-22.0	3.2	20%
14375	0.479	15.2	5.8	43.3	-13.3	3.3	31%
14375	0.513	15.5	5.8	44.0	-12.3	3.3	31%
14376	0.492	14.6	6.0	43.5	-21.3	3.5	32%
14376	0.493	14.8	5.8	43.5	-20.9	3.4	32%
14377	0.463	15.3	5.8	43.9	-21.1	3.3	34%
14377	0.568	15.2	5.9	43.2	-21.0	3.3	34%
14378	0.521	14.7	6.0	42.9	-21.0	3.4	28%
14378	0.463	15.3	6.4	44.2	-21.1	3.4	28%
14379	0.36	15.1	5.1	43.4	-20.6	3.4	26%
14379	0.525	15.3	5.4	43.4	-20.5	3.3	26%

APPENDIX 5

Collagen yields, C: N ratios , %C/%N

UCT specimen number	Wt (mg)	%N	Std corrected $\delta^{15}N$	%C	Std corrected $\delta^{13}C$	C:N ratio elemental	Collagen yield
14380	0.531	14.1	6.2	40.8	-20.7	3.4	20%
14380	0.477	14.9	6.3	42.9	-20.9	3.4	20%
14696	0.509	15.8	5.4	43.2	-20.8	3.2	21%
14696	0.484	16.1	5.3	43.9	-20.6	3.2	21%
15269	0.454	14.9	17.2	41.4	-14.2	3.3	16%
15269	0.588	15.9	17.2	43.5	-15.8	3.2	16%
15270	0.559	16.3	6.5	44.9	-18.8	3.2	28%
15270	0.494	16.1	6.7	44.0	-18.5	3.2	28%
15271	0.514	15.8	7.9	43.3	-10.6	3.2	24%
15271	0.538	20.2	8.0	55.0	-10.7	3.2	24%
15273	0.46	15.6	11.0	42.4	-21.5	3.2	23%
15273	0.484	17.7	11.1	48.0	-21.2	3.2	23%
15274	0.475	14.7	9.9	44.5	-20.4	3.5	23%
15274	0.519	14.9	9.4	44.6	-20.1	3.5	23%
15277	0.5	15.4	9.1	44.8	-9.2	3.4	19%
15277	0.55	15.2	8.8	43.2	-8.6	3.3	19%
15278	0.5	14.3	10.8	39.4	-18.2	3.2	21%
15278	0.524	13.8	10.1	37.5	-18.2	3.2	21%
15284	0.549	15.9	10.8	43.6	-18.3	3.2	16%
15284	0.481	16.2	11.0	44.5	-18.4	3.2	16%
15332	0.521	15.4	6.9	42.9	-21.4	3.2	23%
15332	0.485	15.6	6.6	43.1	-21.4	3.2	23%
15333	0.509	16.3	3.8	43.9	-23.6	3.2	26%
15333	0.488	16.2	3.9	43.8	-23.4	3.2	26%
15334	0.488	15.8	3.4	43.4	-24.6	3.2	28%
15334	0.477	18.9	3.1	51.9	-24.9	3.2	28%
15335	0.462	16.1	3.2	44.2	-23.5	3.2	26%
15335	0.488	15.3	2.9	41.8	-23.5	3.2	26%
15336	0.54	16.0	10.8	43.8	-20.1	3.2	23%
15336	0.481	15.8	10.7	43.2	-20.1	3.2	23%
15337	0.477	15.5	8.5	42.6	-19.0	3.2	25%
15337	0.516	15.8	8.8	43.1	-18.9	3.2	25%
15338	0.496	16.1	4.7	44.1	-20.6	3.2	21%
15338	0.47	12.4	4.4	33.7	-20.6	3.2	21%
15339	0.497	15.8	6.1	43.4	-20.8	3.2	22%
15339	0.509	16.0	5.6	44.0	-20.7	3.2	22%
15340	0.496	16.0	4.5	44.6	-21.4	3.2	25%
15340	0.476	16.2	4.6	44.5	-21.6	3.2	25%
15341	0.5	15.5	4.4	43.5	-21.4	3.3	28%
15341	0.491	15.2	4.7	42.2	-21.4	3.3	28%
15342	0.529	15.1	5.2	43.4	-10.1	3.4	21%
15342	0.462	15.2	5.5	43.3	-10.0	3.3	21%
15343	0.527	15.3	8.0	42.7	-21.1	3.3	24%
15343	0.49	15.7	8.1	43.6	-21.0	3.2	24%
15344	0.48	16.2	9.0	44.5	-20.8	3.2	24%
15344	0.502	15.7	8.7	42.8	-21.0	3.2	24%
15345	0.513	15.7	3.7	43.2	-21.0	3.2	24%
15345	0.457	15.7	3.9	43.1	-20.6	3.2	24%
15346	0.457	15.1	7.0	41.5	-19.2	3.2	28%
15346	0.551	15.3	7.1	42.1	-19.2	3.2	28%
15347	0.464	15.1	5.8	43.8	-20.6	3.4	23%
15347	0.466	15.3	5.8	41.5	-20.5	3.2	23%
15348	0.484	15.3	6.0	42.1	-22.1	3.2	21%

APPENDIX 5

Collagen yields, C: N ratios , %C/%N

UCT specimen number	Wt (mg)	%N	Std corrected $\delta^{15}N$	%C	Std corrected $\delta^{13}C$	C:N ratio elemental	Collagen yield
15348	0.529	14.1	5.7	38.3	-22.1	3.2	21%
15349	0.53	15.9	6.3	43.4	-23.0	3.2	24%
15349	0.495	14.5	6.4	39.5	-22.7	3.2	24%
15350	0.518	16.4	5.2	45.9	-20.9	3.3	29%
15350	0.471	15.5	5.4	42.5	-20.7	3.2	29%
15352	0.574	15.9	3.7	44.3	-22.2	3.2	26%
15352	0.553	15.7	3.4	43.4	-22.3	3.2	26%
15353	0.47	14.4	3.2	40.4	-21.6	3.3	27%
15353	0.478	15.4	3.2	42.3	-21.9	3.2	27%
15354	0.506	15.0	5.8	42.2	-21.6	3.3	23%
15354	0.538	15.6	5.2	43.1	-21.6	3.2	23%
15355	0.532	15.4	7.2	42.4	-19.3	3.2	28%
15355	0.52	15.9	7.5	43.7	-19.3	3.2	28%
15356	0.485	15.6	6.8	44.4	-20.2	3.3	27%
15356	0.47	15.1	6.4	42.5	-20.0	3.3	27%
15357	0.511	15.9	4.8	44.0	-21.3	3.2	26%
15357	0.485	15.8	4.8	43.6	-21.3	3.2	26%
15358	0.527	15.6	5.7	43.9	-20.8	3.3	25%
15358	0.53	15.6	6.1	42.9	-20.7	3.2	25%
15359	0.526	13.5	7.3	37.0	-19.0	3.2	26%
15359	0.466	15.8	7.1	43.1	-19.1	3.2	26%
15360	0.467	14.7	5.2	41.7	-21.7	3.3	31%
15360	0.407	15.7	5.1	44.0	-21.8	3.3	31%
15361	0.55	15.4	3.9	43.2	-21.4	3.3	20%
15361	0.531	15.8	3.8	44.2	-21.2	3.3	20%
15362	0.488	15.9	8.5	43.8	-15.2	3.2	24%
15362	0.498	15.8	8.4	43.4	-15.0	3.2	24%
15363	0.474	16.0	8.1	44.2	-16.9	3.2	28%
15363	0.495	18.2	8.0	49.8	-16.9	3.2	28%
15364	0.547	15.3	4.9	43.7	-14.8	3.3	29%
15364	0.469	15.1	4.8	42.8	-15.0	3.3	29%
15365	0.52	14.6	11.0	42.4	-16.8	3.4	29%
15365	0.562	14.7	10.9	42.7	-16.4	3.4	29%
15366	0.533	15.2	6.2	43.1	-22.3	3.3	24%
15366	0.563	15.6	5.9	43.5	-21.7	3.3	24%
15367	0.551	15.1	4.4	41.4	-20.4	3.2	24%
15367	0.511	13.4	4.5	36.6	-20.7	3.2	24%
15368	0.468	15.4	6.3	45.0	-19.9	3.4	27%
15368	0.481	14.7	5.8	41.8	-19.8	3.3	27%
15370	0.486	15.2	3.3	42.4	-19.8	3.3	16%
15370	0.47	15.2	3.2	42.3	-19.8	3.2	16%
15371	0.539	15.9	8.2	43.8	-21.0	3.2	28%
15371	0.487	15.7	7.6	43.4	-20.7	3.2	28%
15372	0.467	14.7	4.9	41.2	-9.9	3.3	20%
15372	0.489	15.6	5.1	42.8	-9.4	3.2	20%
15373	0.465	15.5	6.5	42.5	-11.7	3.2	19%
15373	0.535	15.7	6.7	42.9	-11.9	3.2	19%
15374	0.52	18.1	11.8	50.0	-9.6	3.2	28%
15374	0.457	15.8	11.9	43.5	-9.8	3.2	28%
15375	0.542	15.2	6.8	42.4	-21.1	3.3	21%
15375	0.506	15.5	6.4	42.7	-21.0	3.2	21%
15376	0.535	15.0	3.0	41.9	-19.6	3.3	16%
15376	0.485	15.2	2.9	42.3	-19.6	3.3	16%

APPENDIX 5

Collagen yields, C: N ratios , %C/%N

UCT specimen number	Wt (mg)	%N	Std corrected $\delta^{15}N$	%C	Std corrected $\delta^{13}C$	C:N ratio elemental	Collagen yield
15378	0.528	16.1	5.1	44.1	-20.5	3.2	26%
15378	0.519	15.9	4.8	43.4	-20.4	3.2	26%
15379	0.504	13.7	7.9	39.1	-22.0	3.3	27%
15379	0.521	14.0	7.8	39.6	-21.9	3.3	27%
15381	0.466	15.5	3.5	42.4	-22.9	3.2	28%
15381	0.503	15.7	3.7	42.7	-23.1	3.2	28%
15382	0.585	15.7	5.4	43.5	-22.8	3.2	21%
15382	0.465	15.5	5.0	43.2	-22.7	3.2	21%
15383	0.49	15.6	11.2	43.0	-12.8	3.2	24%
15383	0.501	16.1	10.5	44.2	-13.5	3.2	24%
15384	0.472	15.1	3.7	42.2	-21.0	3.3	27%
15384	0.457	15.4	3.4	43.1	-21.2	3.3	27%
15385	0.505	15.8	7.0	43.7	-20.2	3.2	25%
15385	0.548	15.6	7.0	42.8	-20.4	3.2	25%
15386	0.523	15.9	5.7	44.0	-21.0	3.2	24%
15386	0.464	16.1	5.2	44.1	-20.8	3.2	24%
15404	0.466	13.9	12.3	38.2	-19.4	3.2	19%
15404	0.474	16.5	11.9	45.1	-19.4	3.2	19%
15405	0.492	15.8	11.0	45.2	-19.0	3.3	26%
15405	0.572	14.7	12.0	41.3	-18.7	3.3	26%
15406	0.453	14.7	11.0	40.7	-19.7	3.2	23%
15406	0.411	15.8	10.6	43.4	-19.7	3.2	23%
15407	0.552	16.5	11.7	45.5	-18.4	3.2	24%
15407	0.501	15.7	11.8	43.3	-18.0	3.2	24%
15408	0.573	15.5	11.3	42.6	-19.6	3.2	20%
15408	0.411	15.1	10.5	41.6	-19.8	3.2	20%
15409	0.5	13.1	11.4	38.1	-20.6	3.4	23%
15409	0.564	14.4	10.5	41.1	-20.4	3.3	23%
15409	0.458	14.8	10.8	41.5	-20.4	3.3	23%
15409	0.401	15.1	9.7	42.2	-20.6	3.3	23%
15410	0.481	14.7	11.6	40.9	-18.5	3.3	23%
15410	0.494	16.1	11.5	44.3	-18.6	3.2	23%
15411	0.457	14.5	12.4	40.4	-18.6	3.3	22%
15411	0.522	15.4	11.3	42.5	-18.7	3.2	22%
15412	0.503	16.1	10.8	44.5	-20.1	3.2	21%
15412	0.4	16.0	9.6	44.2	-20.1	3.2	21%
15413	0.44	14.2	7.6	42.8	-19.0	3.5	24%
15413	0.521	15.9	7.9	45.0	-18.7	3.3	24%
15414	0.499	15.2	10.3	42.3	-20.3	3.2	23%
15414	0.473	15.4	9.3	42.2	-21.1	3.2	23%
15415	0.495	15.5	12.4	42.7	-17.6	3.2	20%
15415	0.473	15.4	12.5	42.1	-17.6	3.2	20%
15416	0.512	16.7	11.1	45.8	-18.9	3.2	20%
15416	0.478	15.9	11.2	43.7	-18.9	3.2	20%
15417	0.542	15.3	6.5	41.9	-19.9	3.2	17%
15417	0.474	16.1	6.6	44.1	-20.1	3.2	17%
15418	0.543	15.6	12.5	43.1	-19.5	3.2	23%
15418	0.466	15.0	12.9	41.3	-19.2	3.2	23%
15418	0.586	15.6	12.7	42.8	-19.5	3.2	23%
15419	0.473	15.6	12.4	43.4	-19.3	3.2	25%
15419	0.466	15.7	12.4	43.4	-19.3	3.2	25%
15420	0.577	15.2	10.3	41.8	-18.1	3.2	22%
15420	0.407	16.6	10.3	45.2	-18.0	3.2	22%

APPENDIX 5

Collagen yields, C: N ratios , %C/%N

UCT specimen number	Wt (mg)	%N	Std corrected $\delta^{15}N$	%C	Std corrected $\delta^{13}C$	C:N ratio elemental	Collagen yield
15421	0.517	13.8	9.4	38.5	-15.1	3.3	22%
15421	0.423	14.8	9.3	41.0	-14.8	3.2	22%
15422	0.481	14.8	9.6	42.2	-14.6	3.3	26%
15422	0.464	14.4	9.7	40.6	-14.3	3.3	26%
15423	0.395	15.2	4.3	41.8	-20.1	3.2	23%
15423	0.44	16.4	4.4	45.2	-20.1	3.2	23%
15424	0.512	14.3	13.2	40.2	-19.2	3.3	15%
15424	0.45	13.3	13.4	37.1	-19.4	3.3	15%
15425	0.458	15.1	12.6	41.6	-18.0	3.2	20%
15425	0.582	15.4	12.3	42.1	-17.9	3.2	20%
15426	0.451	15.6	4.1	43.5	-20.7	3.3	22%
15426	0.453	14.9	4.0	41.3	-20.7	3.2	22%
15427	0.412	15.0	4.1	41.1	-19.9	3.2	15%
15427	0.53	15.5	4.1	42.5	-19.9	3.2	15%
15428	0.422	15.1	12.5	41.9	-19.8	3.2	23%
15428	0.47	15.3	12.4	42.3	-19.9	3.2	23%
15429	0.471	15.5	12.9	42.5	-19.3	3.2	5%
15429	0.475	15.0	13.0	41.1	-19.4	3.2	5%
15430	0.425	14.9	11.7	41.3	-8.3	3.2	25%
15430	0.413	15.4	10.8	42.4	-8.0	3.2	25%
15431	0.506	15.1	11.9	41.6	-9.0	3.2	23%
15431	0.401	16.4	11.0	44.6	-8.6	3.2	23%
15432	0.54	14.5	10.5	40.1	-9.4	3.2	24%
15432	0.477	15.6	10.5	42.5	-9.0	3.2	24%
15433	0.559	16.4	11.6	46.3	-7.9	3.3	23%
15433	0.485	16.8	10.8	47.1	-7.6	3.3	23%
15434	0.475	15.4	11.5	41.9	-7.6	3.2	26%
15434	0.494	15.6	11.4	42.4	-7.9	3.2	26%
15435	0.579	16.2	10.7	44.6	-7.3	3.2	23%
15435	0.506	16.4	10.8	45.0	-7.5	3.2	23%
15437	0.46	14.9	11.8	41.5	-20.0	3.3	28%
15437	0.55	15.6	11.7	43.4	-19.8	3.2	28%
15438	0.527	15.0	10.7	41.6	-20.3	3.2	25%
15438	0.577	15.6	11.0	43.1	-19.9	3.2	25%
15439	0.462	16.2	5.2	44.9	-7.5	3.2	21%
15439	0.52	17.2	4.2	47.1	-7.4	3.2	21%
15440	0.437	15.2	10.8	41.8	-22.3	3.2	25%
15440	0.514	15.4	10.6	42.2	-22.9	3.2	25%
15441	0.502	16.8	11.1	46.0	-9.6	3.2	25%
15441	0.532	16.7	11.2	45.8	-10.1	3.2	25%
15582	0.54	15.3	9.4	42.9	-22.8	3.3	21%
15582	0.516	15.4	9.3	42.5	-22.9	3.2	21%
15593	0.484	14.3	6.3	40.6	-19.0	3.3	23%
15593	0.533	17.2	5.8	47.9	-19.0	3.2	23%
15594	0.479	15.4	5.6	44.0	-19.2	3.3	24%
15594	0.483	15.4	5.6	43.4	-19.3	3.3	24%
15595	0.519	14.6	9.4	40.8	-17.5	3.3	25%
15595	0.467	15.6	9.7	43.6	-17.5	3.3	25%
15596	0.526	14.9	10.2	42.2	-15.6	3.3	26%
15596	0.544	14.1	10.6	40.1	-15.2	3.3	26%
15597	0.469	14.4	11.1	40.3	-18.3	3.3	25%
15597	0.501	13.5	11.0	37.7	-18.8	3.3	25%
15598	0.549	14.7	10.5	41.9	-19.2	3.3	30%

APPENDIX 5

Collagen yields, C: N ratios , %C/%N

UCT specimen number	Wt (mg)	%N	Std corrected $\delta^{15}N$	%C	Std corrected $\delta^{13}C$	C:N ratio elemental	Collagen yield
15598	0.523	15.8	10.3	44.0	-18.7	3.3	30%
15599	0.484	14.6	10.6	42.7	-17.2	3.4	24%
15599	0.549	15.3	10.7	43.5	-17.2	3.3	24%
15600	0.467	14.1	10.3	40.0	-16.6	3.3	27%
15600	0.483	16.4	10.3	46.0	-15.7	3.3	27%
15601	0.458	14.4	10.8	39.8	-18.9	3.2	28%
15601	0.488	14.7	10.5	40.7	-18.3	3.2	28%
15615	0.538	14.3	5.7	39.9	-20.7	3.2	29%
15615	0.472	15.7	5.9	43.3	-20.3	3.2	29%
15616	0.539	14.5	5.9	40.6	-20.7	3.3	25%
15616	0.521	15.6	5.8	43.2	-20.3	3.2	25%
15617	0.517	14.4	5.5	39.8	-20.1	3.2	25%
15617	0.473	13.6	5.8	37.6	-20.1	3.2	25%
15618	0.471	14.0	4.8	39.3	-21.0	3.3	26%
15618	0.505	17.0	5.3	47.5	-20.4	3.3	26%
15619	0.524	14.3	5.3	39.8	-20.1	3.3	26%
15619	0.518	15.6	5.1	43.3	-20.3	3.2	26%
15620	0.49	16.0	4.7	44.4	-19.8	3.3	24%
15620	0.492	15.6	4.9	43.2	-19.9	3.2	24%
15621	0.482	14.6	5.7	40.1	-19.6	3.2	6%
15621	0.534	15.8	6.0	43.5	-19.7	3.2	6%
15622	0.461	14.5	5.2	45.0	-21.4	3.6	30%
15623	0.509	14.3	5.5	40.2	-20.8	3.3	27%
15623	0.532	18.1	5.4	50.9	-20.4	3.3	27%
15624	0.494	14.2	5.5	40.2	-20.6	3.3	29%
15624	0.472	17.0	5.2	47.3	-20.1	3.3	29%
15636	0.513	15.3	6.6	44.0	-19.1	3.4	30%
15636	0.498	15.4	7.5	44.2	-19.0	3.4	30%
15637	0.509	15.3	8.5	44.3	-19.2	3.4	28%
15637	0.469	15.3	8.8	44.4	-19.3	3.4	28%
15638	0.54	15.4	7.8	43.8	-18.5	3.3	29%
15638	0.553	15.6	7.9	44.0	-18.4	3.3	29%
15639	0.461	13.7	9.5	39.4	-19.3	3.3	25%
15639	0.562	16.0	9.6	45.3	-19.1	3.3	25%
15640	0.516	13.8	6.6	40.2	-19.7	3.4	29%
15640	0.499	15.2	6.5	43.1	-19.3	3.3	29%
15641	0.472	15.3	6.3	44.1	-19.2	3.4	28%
15641	0.565	15.3	5.9	43.8	-19.3	3.3	28%
15642	0.519	13.6	7.7	39.2	-19.7	3.4	26%
15642	0.457	16.3	7.6	46.8	-19.8	3.3	26%
15643	0.529	14.4	8.1	42.6	-20.1	3.5	24%
15643	0.496	15.2	6.6	44.2	-19.7	3.4	24%
15644	0.544	13.3	8.2	40.1	-20.4	3.5	25%
15644	0.498	14.8	8.1	43.9	-20.1	3.5	25%
15645	0.488	15.4	6.7	44.2	-19.7	3.4	29%
15645	0.519	15.4	6.7	44.0	-19.6	3.3	29%
15646	0.495	13.9	7.5	40.6	-19.5	3.4	30%
15646	0.504	15.1	7.4	43.8	-19.7	3.4	30%
15647	0.488	15.1	7.1	44.6	-19.5	3.4	26%
15647	0.492	15.3	6.6	43.9	-19.6	3.4	26%
16061	0.547	14.4	10.3	40.2	-18.6	3.3	26%
16061	0.498	15.1	9.9	42.2	-17.7	3.3	26%
16062	0.502	14.5	5.4	42.1	-20.6	3.4	26%

APPENDIX 5

Collagen yields, C: N ratios , %C/%N

UCT specimen number	Wt (mg)	%N	Std corrected $\delta^{15}N$	%C	Std corrected $\delta^{13}C$	C:N ratio elemental	Collagen yield
16062	0.498	15.2	5.1	43.5	-20.4	3.3	26%
16063	0.534	14.6	5.1	41.7	-20.6	3.3	27%
16063	0.517	15.7	5.4	44.6	-20.6	3.3	27%
16064	0.537	13.6	5.1	37.9	-20.1	3.3	26%
16064	0.48	17.1	5.1	46.8	-20.1	3.2	26%
16065	0.518	13.3	4.5	37.7	-20.8	3.3	26%
16065	0.547	14.2	4.2	39.7	-20.3	3.3	26%
16066	0.468	14.2	5.3	39.5	-19.6	3.2	27%
16066	0.457	17.0	5.4	46.7	-19.5	3.2	27%
16067	0.49	14.2	6.1	39.9	-18.8	3.3	27%
16067	0.556	15.7	5.8	44.0	-19.0	3.3	27%
16068	0.519	14.3	5.2	40.8	-20.3	3.3	27%
16068	0.494	15.3	5.1	42.8	-20.2	3.3	27%
16069	0.458	15.5	4.7	43.1	-20.3	3.2	29%
16069	0.533	14.4	5.3	39.5	-20.2	3.2	29%
16070	0.469	14.0	4.9	38.5	-20.3	3.2	28%
16070	0.531	15.0	4.9	41.2	-20.2	3.2	28%
16071	0.478	14.0	6.7	39.6	-19.7	3.3	30%
16071	0.469	16.0	5.8	44.6	-19.8	3.3	30%
16072	0.472	15.4	4.2	43.1	-20.1	3.3	25%
16072	0.547	15.5	4.2	43.4	-20.2	3.3	25%
16073	0.481	14.4	4.8	39.7	-20.3	3.2	25%
16073	0.507	17.1	4.9	47.1	-20.4	3.2	25%
16074	0.501	14.3	9.2	40.4	-21.3	3.3	27%
16074	0.527	13.7	9.1	38.7	-21.3	3.3	27%
16075	0.536	15.9	9.4	44.3	-21.5	3.3	25%
16076	0.57	15.1	6.0	42.9	-21.1	3.3	29%
16076	0.525	15.3	5.9	43.4	-21.1	3.3	29%
16077	0.573	15.5	9.2	44.3	-19.1	3.4	28%
16077	0.562	15.3	9.3	43.9	-19.3	3.3	28%
16078	0.457	16.0	5.8	45.6	-20.2	3.3	28%
16078	0.507	15.5	5.2	43.5	-20.5	3.3	28%
16079	0.488	15.5	10.1	43.6	-15.8	3.3	27%
16079	0.54	15.6	10.2	43.9	-15.5	3.3	27%
16080	0.468	14.4	10.6	40.1	-18.7	3.3	26%
16080	0.5	16.7	9.5	46.2	-18.8	3.2	26%
16081	0.512	13.9	8.1	40.6	-18.6	3.4	30%
16081	0.49	14.8	7.7	43.0	-18.6	3.4	30%
16082	0.551	13.6	9.6	39.3	-18.6	3.4	27%
16082	0.563	13.8	9.9	39.6	-18.8	3.4	27%
16083	0.528	15.3	8.9	43.7	-18.8	3.3	30%
16083	0.491	15.3	8.8	43.6	-18.7	3.3	30%
16084	0.546	15.1	7.9	44.0	-18.8	3.4	30%
16084	0.567	15.2	8.3	44.1	-18.6	3.4	30%
16155	0.556	14.1	6.4	39.5	-20.7	3.3	26%
16155	0.478	15.9	6.1	44.2	-21.1	3.2	26%
16156	0.55	13.9	6.1	39.1	-20.7	3.3	21%
16156	0.491	13.8	5.8	38.5	-21.0	3.3	21%
16157	0.516	14.2	5.9	39.9	-20.8	3.3	26%
16157	0.493	16.3	5.7	45.6	-20.6	3.3	26%
16158	0.552	13.8	5.8	38.3	-21.3	3.2	27%
16158	0.542	14.2	5.7	39.3	-21.2	3.2	27%
16159	0.467	14.9	5.8	41.6	-20.9	3.3	28%

APPENDIX 5

Collagen yields, C: N ratios , %C/%N

UCT specimen number	Wt (mg)	%N	Std corrected $\delta^{15}N$	%C	Std corrected $\delta^{13}C$	C:N ratio elemental	Collagen yield
16159	0.569	16.2	5.5	44.9	-21.3	3.2	28%
16160	0.475	14.2	6.0	40.5	-21.1	3.3	24%
16160	0.457	16.1	6.2	45.2	-21.5	3.3	24%
16161	0.472	15.1	6.1	43.1	-20.9	3.3	26%
16161	0.454	15.3	6.1	43.3	-20.8	3.3	26%
16162	0.506	15.4	4.3	43.0	-20.8	3.3	24%
16162	0.545	15.6	4.4	43.4	-20.9	3.3	24%
16163	0.481	14.0	5.0	40.3	-20.8	3.4	27%
16163	0.562	15.4	4.9	44.0	-20.5	3.3	27%
16164	0.503	14.8	4.7	41.2	-20.6	3.3	22%
16164	0.455	15.8	4.8	43.7	-20.7	3.2	22%
16165	0.475	13.3	4.1	38.2	-21.3	3.4	29%
16165	0.528	14.0	4.0	40.1	-21.3	3.3	29%
16166	0.521	14.2	4.4	39.9	-21.2	3.3	28%
16166	0.532	13.1	4.2	36.7	-21.3	3.3	28%
16167	0.477	16.1	4.6	44.8	-21.4	3.2	22%
16167	0.495	15.6	4.3	43.1	-21.3	3.2	22%
16168	0.542	15.5	4.4	42.9	-21.1	3.2	24%
16168	0.532	15.7	4.3	42.7	-21.3	3.2	24%
16169	0.487	14.4	4.3	40.2	-21.4	3.3	25%
16169	0.462	15.6	3.9	43.2	-21.3	3.2	25%
16170	0.475	15.7	4.7	44.0	-21.0	3.3	25%
16170	0.523	15.5	4.1	43.0	-21.1	3.2	25%
16171	0.507	14.4	5.7	40.4	-20.7	3.3	14%
16171	0.469	16.8	5.7	46.4	-20.8	3.2	14%
16173	0.453	15.2	4.3	42.5	-21.0	3.3	26%
16173	0.537	15.0	4.4	42.0	-21.1	3.3	26%
16174	0.485	14.5	4.6	40.3	-21.4	3.3	24%
16174	0.539	16.1	4.4	44.8	-21.4	3.2	24%
16175	0.494	14.2	5.0	40.2	-20.8	3.3	27%
16175	0.569	15.9	5.0	44.7	-20.6	3.3	27%
16176	0.536	13.8	4.1	38.9	-21.2	3.3	24%
16176	0.464	16.9	4.1	47.6	-21.0	3.3	24%
16177	0.542	15.5	3.5	43.2	-21.2	3.3	26%
16177	0.508	15.5	3.5	43.0	-21.3	3.2	26%
16178	0.532	14.0	4.1	39.3	-21.3	3.3	28%
16178	0.543	14.2	3.9	39.7	-21.1	3.3	28%
16179	0.532	14.3	3.9	39.7	-21.4	3.2	27%
16179	0.544	15.3	3.8	42.3	-21.2	3.2	27%
16180	0.522	15.4	6.8	43.4	-18.8	3.3	23%
16180	0.505	15.5	6.7	42.7	-18.6	3.2	23%
16181	0.517	15.2	8.2	44.3	-19.2	3.4	30%
16181	0.49	15.1	7.0	43.0	-19.3	3.3	30%
16182	0.512	15.3	6.1	43.5	-19.6	3.3	19%
16182	0.569	15.5	6.1	43.9	-19.7	3.3	19%
16183	0.52	15.5	6.8	45.5	-20.0	3.4	26%
16183	0.532	13.3	6.6	38.3	-19.8	3.4	26%
16184	0.563	15.5	14.4	43.5	-18.2	3.3	27%
16184	0.571	15.4	14.2	42.7	-18.4	3.2	27%
16185	0.466	15.4	6.9	44.4	-19.4	3.4	30%
16185	0.477	15.3	7.2	44.2	-19.5	3.4	30%
16186	0.568	15.3	6.4	44.5	-19.8	3.4	27%
16186	0.515	14.9	6.8	43.2	-19.8	3.4	27%

APPENDIX 5

Collagen yields, C: N ratios , %C/%N

UCT specimen number	Wt (mg)	%N	Std corrected $\delta^{15}N$	%C	Std corrected $\delta^{13}C$	C:N ratio elemental	Collagen yield
16187	0.512	14.5	7.1	41.6	-19.6	3.4	30%
16187	0.457	15.3	6.6	43.7	-19.4	3.3	30%
16188	0.497	15.1	6.3	43.4	-19.6	3.4	27%
16188	0.506	15.5	6.0	43.3	-19.6	3.3	27%
16189	0.504	15.3	7.4	44.7	-19.2	3.4	29%
16189	0.482	15.1	7.2	43.9	-19.3	3.4	29%
16190	0.542	15.8	6.8	44.0	-21.1	3.3	28%
16190	0.46	15.7	6.5	43.2	-21.4	3.2	28%
16191	0.527	13.9	7.3	40.9	-19.7	3.4	30%
16191	0.513	14.8	7.3	42.5	-19.5	3.4	30%
16192	0.49	15.1	7.2	45.7	-19.5	3.5	30%
16192	0.457	15.1	7.0	44.1	-19.7	3.4	30%
16193	0.548	15.3	7.5	44.5	-19.8	3.4	28%
16193	0.548	15.2	7.4	44.0	-20.0	3.4	28%
16194	0.567	15.2	7.2	43.9	-19.5	3.4	29%
16194	0.542	15.3	7.1	43.9	-19.3	3.4	29%
16195	0.529	14.5	10.9	40.8	-19.3	3.3	27%
16195	0.528	13.3	10.3	37.4	-19.1	3.3	27%
16196	0.504	13.9	7.7	40.4	-19.7	3.4	29%
16196	0.551	14.5	8.2	41.2	-19.4	3.3	29%
16197	0.502	14.2	7.7	40.9	-19.6	3.4	29%
16197	0.502	13.1	7.2	37.2	-19.5	3.3	29%
16198	0.48	14.1	8.7	41.2	-20.4	3.4	29%
16198	0.562	13.8	8.5	40.0	-20.0	3.4	29%
16199	0.516	13.7	7.2	39.4	-19.6	3.4	20%
16199	0.519	15.1	7.3	43.2	-19.6	3.3	20%
16200	0.466	14.8	6.7	44.7	-19.9	3.5	28%
16200	0.554	15.2	6.3	44.4	-19.9	3.4	28%
16201	0.516	14.2	4.3	39.3	-21.1	3.2	25%
16201	0.496	15.7	4.3	43.0	-20.7	3.2	25%
16202	0.506	14.4	10.4	40.2	-18.9	3.3	24%
16202	0.47	15.5	10.4	43.5	-18.5	3.3	24%
16203	0.477	15.4	8.5	43.3	-17.9	3.3	27%
16203	0.467	15.5	8.8	43.6	-17.9	3.3	27%
16204	0.562	13.7	7.5	38.4	-19.4	3.3	26%
16204	0.526	17.0	7.6	47.5	-19.0	3.3	26%
16205	0.554	15.4	7.8	43.4	-19.7	3.3	25%
16205	0.479	15.7	7.2	43.2	-19.7	3.2	25%
16206	0.527	13.7	7.7	39.9	-19.2	3.4	25%
16206	0.557	15.1	7.5	43.8	-19.1	3.4	25%
16213	0.489	15.7	9.7	43.0	-11.4	3.2	23%
16213	0.462	15.7	9.9	43.0	-11.7	3.2	23%
16214	0.465	15.4	10.4	43.6	-13.5	3.3	19%
16214	0.507	15.5	10.6	43.7	-14.2	3.3	19%
16215	0.486	15.4	8.6	43.4	-19.2	3.3	24%
16215	0.468	15.4	8.4	43.2	-19.5	3.3	24%
16216	0.519	10.7	10.3	31.0	-10.0	3.4	26%
16216	0.493	13.8	10.6	39.4	-9.7	3.3	26%
16217	0.486	15.8	8.4	44.5	-19.0	3.3	26%
16217	0.501	15.6	8.4	43.7	-18.8	3.3	26%
16218	0.462	10.5	10.4	31.2	-15.9	3.5	23%
16218	0.474	15.4	10.2	43.6	-16.2	3.3	23%
16219	0.471	15.0	11.7	41.4	-17.5	3.2	25%

APPENDIX 5

Collagen yields, C: N ratios , %C/%N

UCT specimen number	Wt (mg)	%N	Std corrected $\delta^{15}N$	%C	Std corrected $\delta^{13}C$	C:N ratio elemental	Collagen yield
16219	0.53	15.6	11.6	42.8	-17.3	3.2	25%
16220	0.468	14.6	10.1	41.1	-9.6	3.3	24%
16220	0.502	14.5	10.3	40.5	-9.8	3.3	24%
16236	0.456	15.4	10.8	43.3	-20.2	3.3	21%
16236	0.488	15.7	10.7	43.3	-20.0	3.2	21%
16237	0.49	16.2	12.1	45.6	-20.8	3.3	27%
16237	0.494	15.6	11.8	44.0	-20.7	3.3	27%
16370	0.526	14.7	6.5	41.2	-13.0	3.3	26%
16370	0.496	15.6	6.6	43.5	-13.7	3.3	26%
16371	0.56	15.7	10.0	43.5	-19.8	3.2	22%
16371	0.472	15.5	10.1	42.9	-20.2	3.2	22%
16372	0.478	16.0	5.8	44.3	-8.5	3.2	21%
16372	0.553	18.0	5.5	49.6	-8.7	3.2	21%
16373	0.581	16.6	10.9	47.1	-20.0	3.3	20%
16373	0.55	15.6	11.2	43.6	-20.8	3.3	20%
16374	0.478	16.8	11.6	47.9	-21.0	3.3	23%
16374	0.558	15.2	11.5	43.2	-20.7	3.3	23%
16375	0.5	16.0	10.1	44.6	-21.0	3.2	19%
16375	0.577	15.6	9.1	43.2	-21.7	3.2	19%
16376	0.519	15.4	11.4	42.9	-17.5	3.2	22%
16376	0.555	15.8	10.3	43.6	-18.4	3.2	22%
16377	0.547	15.2	13.7	43.1	-19.8	3.3	21%
16377	0.513	14.8	13.7	41.9	-19.5	3.3	21%
16378	0.475	15.4	11.6	42.9	-18.5	3.3	21%
16378	0.464	14.8	11.6	41.2	-18.2	3.2	21%
16379	0.524	16.5	10.8	45.4	-21.1	3.2	
16379	0.417	15.7	10.1	43.5	-21.1	3.2	
16380	0.501	13.3	5.5	36.6	-10.0	3.2	18%
16380	0.478	15.9	5.9	43.4	-9.7	3.2	18%
16381	0.5	15.2	10.2	43.5	-21.5	3.3	18%
16381	0.54	14.8	10.2	42.0	-21.4	3.3	18%
16382	0.506	12.9	8.9	35.9	-22.4	3.2	20%
16382	0.492	15.6	8.9	43.0	-22.4	3.2	20%
16383	0.497	15.7	11.2	43.5	-19.4	3.2	20%
16383	0.516	15.3	11.6	42.3	-18.4	3.2	20%
16384	0.575	16.7	6.5	45.7	-21.7	3.2	23%
16384	0.508	16.4	5.9	44.9	-21.3	3.2	23%
16385	0.492	15.7	10.9	43.3	-16.7	3.2	25%
16385	0.497	15.7	10.9	43.0	-16.9	3.2	25%
16386	0.467	14.9	11.3	42.2	-14.7	3.3	23%
16386	0.414	15.2	11.4	42.8	-14.4	3.3	23%
16387	0.483	14.9	10.6	42.2	-15.9	3.3	26%
16387	0.576	15.2	10.4	42.9	-15.7	3.3	26%
16388	0.512	15.2	9.2	42.3	-18.5	3.2	27%
16388	0.573	16.3	9.1	45.1	-18.2	3.2	27%
16389	0.478	15.9	10.3	43.8	-17.1	3.2	28%
16389	0.506	15.8	10.6	43.1	-17.4	3.2	28%
16390	0.498	14.6	10.1	41.2	-14.6	3.3	22%
16390	0.568	14.9	9.8	41.1	-13.7	3.2	22%
16391	0.519	15.2	10.9	42.8	-16.7	3.3	23%
16391	0.582	15.4	10.4	42.6	-16.2	3.2	23%
16392	0.495	15.1	10.7	42.2	-16.0	3.3	25%
16392	0.586	15.3	10.2	42.2	-16.9	3.2	25%

APPENDIX 5

Collagen yields, C: N ratios , %C/%N

UCT specimen number	Wt (mg)	%N	Std corrected $\delta^{15}N$	%C	Std corrected $\delta^{13}C$	C:N ratio elemental	Collagen yield
16393	0.542	15.3	11.1	43.5	-17.5	3.3	23%
16393	0.578	15.4	11.1	43.6	-16.5	3.3	23%
16394	0.541	15.0	11.3	43.2	-15.8	3.4	27%
16394	0.504	13.6	10.7	38.4	-14.8	3.3	27%
16395	0.482	17.4	11.5	50.4	-16.5	3.4	21%
16395	0.468	14.7	11.4	42.6	-16.2	3.4	21%

APPENDIX 6

Tests of normality: Kolmogorov-Smirnov and Shapiro-Wilk

Tests of Normality

		Kolmogorov-Smirnov[a]			Shapiro-Wilk			Result
		Statistic	df	Sig.	Statistic	df	Sig.	
Enamel Apatite	$\delta^{13}C_{enamel}$	0.159	514	0.000	0.886	514	0.000	non-normal
	$\delta^{18}O$	0.064	514	0.000	0.981	514	0.000	non-normal
Bone Collagen	$\delta^{15}N$	0.096	464	0.000	0.967	464	0.000	non-normal
	$\delta^{13}C_{collagen}$	0.206	464	0.000	0.854	464	0.000	non-normal

a. Lilliefors Significance Correction

Tests of Normality

			Kolmogorov-Smirnov[a]			Shapiro-Wilk			Result
FeederType			Statistic	df	Sig.	Statistic	df	Sig.	
Browser	Enamel Apatite	$\delta^{13}C_{enamel}$	0.121	124	0.000	0.945	124	0.000	non-normal
		$\delta^{18}O$	0.103	124	0.003	0.967	124	0.004	non-normal
Browser	Bone collagen	$\delta^{15}N$	0.141	104	0.000	0.942	104	0.000	non-normal
		$\delta^{13}C_{collagen}$	0.134	104	0.000	0.882	104	0.000	non-normal
Grazer	Enamel Apatite	$\delta^{13}C_{enamel}$	0.108	129	0.001	0.935	129	0.000	non-normal
		$\delta^{18}O$	0.155	129	0.000	0.910	129	0.000	non-normal
Grazer	Bone collagen	$\delta^{15}N$	0.132	129	0.000	0.927	129	0.000	non-normal
		$\delta^{13}C_{collagen}$	0.097	129	0.005	0.944	129	0.000	non-normal
Mixed	Enamel Apatite	$\delta^{13}C_{enamel}$	0.113	68	0.031	0.953	68	0.013	non-normal
		$\delta^{18}O$	0.098	68	0.173	0.969	68	0.093	normal
Mixed	Bone collagen	$\delta^{15}N$	0.150	41	0.021	0.895	41	0.001	non-normal
		$\delta^{13}C_{collagen}$	0.143	41	0.034	0.955	41	0.105	normal
Carnivore	Enamel Apatite	$\delta^{13}C_{enamel}$	0.146	33	0.074	0.971	33	0.495	normal
		$\delta^{18}O$	0.156	33	0.041	0.939	33	0.065	normal
Carnivore	Bone collagen	$\delta^{15}N$	0.116	32	.200*	0.944	32	0.098	normal
		$\delta^{13}C_{collagen}$	0.169	32	0.021	0.901	32	0.006	non-normal
Omnivore	Enamel Apatite	$\delta^{13}C_{enamel}$	0.179	160	0.000	0.773	160	0.000	non-normal
		$\delta^{18}O$	0.083	160	0.009	0.946	160	0.000	non-normal
Omnivore	Bone collagen	$\delta^{15}N$	0.114	158	0.000	0.926	158	0.000	non-normal
		$\delta^{13}C_{collagen}$	0.201	158	0.000	0.711	158	0.000	non-normal

*. This is a lower bound of the true significance.

a. Lilliefors Significance Correction

APPENDIX 7

$\delta^{13}C$ and $\delta^{18}O$ results from enamel apatite and $\delta^{13}C$ and $\delta^{15}N$ results from bone collagen for all specimens: An average is reported for duplicate results from one individual

UCT	Type	Feeder Type	Species	Common_name	Biome	Location	N Enamel	Tooth sampled	$\delta^{13}C_{enamel}$	Enamel Fossil fuel adjusted	$\delta^{18}O_{enamel}$	N Collagen	$\delta^{15}N_{collagen}$	$\delta^{13}C_{collagen}$	Collagen Fossil fuel adjusted	$\Delta_{enamel-collagen}$	Water behaviour: WD OR WI	Evaporation sensitivity: ES or EI	Size: S, M, L, or Ex L	R or H fermenter
14298	Carnivore	Carnivore	*Panthera leo*	Lion	Albany Thicket	Addo national Park	1	M^2	-7.8	-5.8	0.4	2	14.9	-13.5	-11.5	5.6	-	-	-	-
14299	Carnivore	Carnivore	*Crocuta crocuta*	Spotted hyena	Albany Thicket	Addo national Park	1	M^2	-9.9	-7.9	-2.5	2	15.2	-14.8	-12.8	4.9	-	-	-	-
15344	Carnivore	Carnivore	*Felis caracal*	Caracal	Forest	Garden route National Pa	1	M	-18.2	-16.2	-8.8	2	8.9	-20.9	-18.9	2.8	-	-	-	-
15346	Carnivore	Carnivore	*Mellivora capensis*	Honey badger	Forest	Garden route National Pa	1	M	-13.8	-11.8	-5.1	2	7.1	-19.2	-17.2	5.4	-	-	-	-
15356	Carnivore	Carnivore	*Felis caracal*	Caracal	Forest	Garden route National Pa	1	M_1	-13.6	-11.6	-5.5	2	6.6	-20.1	-18.1	6.5	-	-	-	-
15362	Carnivore	Carnivore	*Genetta genetta*	Genet	Forest	Garden route National Pa	1	M^2	-12.3	-10.3	-9.2	2	8.4	-15.1	-13.1	2.8	-	-	-	-
15363	Carnivore	Carnivore	*Panthera pardus*	leopard	Forest	Garden route National Pa	1	M_3	-13.6	-11.6	-2.8	2	8.1	-16.9	-14.9	3.3	-	-	-	-
15380	Carnivore	Carnivore	*Mellivora capensis*	Honey badger	Forest	Garden route National Pa	1	C_1	-14.4	-12.4	-9.2						-	-	-	-
15383	Carnivore	Carnivore	*Otocyon megalotis*	Bateared fox	Forest	Garden route National Pa	1	C_1	-9.7	-7.7	-10.0	2	10.8	-13.1	-11.1	3.4	-	-	-	-
1716	Carnivore	Carnivore	*Vulpes chama*	Cape fox	Fynbos	Robertson	1	C_1	-11.6	-9.6	-0.7	1	14.7	-17.3	-15.3	5.8	-	-	-	-
1717	Carnivore	Carnivore	*Canis mesomelas*	black-backed jackal	Fynbos	Robertson	5	-	-13.3	-11.3	-1.6	2	11.8	-18.4	-16.4	5.0	-	-	-	-
1718	Carnivore	Carnivore	*Canis mesomelas*	black-backed jackal	Fynbos	Robertson	3	-	-9.8	-7.8	-2.2	2	11.3	-13.1	-11.1	3.3	-	-	-	-
1719	Carnivore	Carnivore	*Felis caracal*	Caracal	Fynbos	Caledon	2	-	-14.6	-12.6	-3.4	2	7.3	-19.2	-17.2	4.6	-	-	-	-
1720	Carnivore	Carnivore	*Felis caracal*	Caracal	Fynbos	Bonnievale	3	-	-12.6	-10.6	-2.2	2	11.6	-18.1	-16.1	5.5	-	-	-	-
14127	Carnivore	Carnivore	*Panthera pardus*	leopard	Fynbos	Vrolikheid Nature reserve	1	M_1	-13.7	-11.7	-2.9	2	9.7	-20.5	-18.5	6.7	-	-	-	-
14129	Carnivore	Carnivore	*Panthera pardus*	leopard	Fynbos	Voelvlei Dam, Gouda - Tı	1	M^3	-15.7	-13.7	-2.1	2	9.7	-19.0	-17.0	3.4	-	-	-	-
14131	Carnivore	Carnivore	*Panthera pardus*	leopard	Fynbos	Between george and knys	1	M^3	-16.6	-14.6	-3.6	2	9.4	-19.1	-17.1	2.5	-	-	-	-
14132	Carnivore	Carnivore	*Panthera pardus*	leopard	Fynbos	Southwestern Cape	1	M^3	-15.0	-13.0	-2.1	2	6.9	-20.0	-18.0	5.1	-	-	-	-
14134	Carnivore	Carnivore	*Panthera pardus*	leopard	Fynbos	Redelinghuis	1	M^3	-14.1	-12.1	-0.2	2	11.0	-19.8	-17.8	5.6	-	-	-	-
14135	Carnivore	Carnivore	*Panthera pardus*	leopard	Fynbos	Piketberg	1	M^3	-14.8	-12.8	-3.7	2	10.4	-20.1	-18.1	5.3	-	-	-	-
14136	Carnivore	Carnivore	*Panthera pardus*	leopard	Fynbos	Du toits kloof	1	M^3	-15.6	-13.6	-2.5	2	5.2	-20.8	-18.8	5.2	-	-	-	-
16236	Carnivore	Carnivore	*Proteles cristata*	Aardwolf	Fynbos	Cederberg	1	C^1	-13.5	-11.5	0.9	2	10.7	-20.1	-18.1	6.6	-	-	-	-
16237	Carnivore	Carnivore	*Felis caracal*	Caracal	Fynbos	Cederberg	1	M_1	-15.6	-13.6	0.0	2	12.0	-20.7	-18.7	5.1	-	-	-	-
2061	Carnivore	Carnivore	*Otocyon megalotis*	Bateared fox	Nama Karoo	Richmond	1	M^2	-11.4	-9.4	-4.8	2	10.8	-15.1	-13.1	3.8	-	-	-	-
7735	Carnivore	Carnivore	*Felis caracal*	Caracal	Savanna	Kgalagadi National Park	1	C^1	-8.1	-6.1	-1.5	2	13.7	-15.3	-13.3	7.2	-	-	-	-
7736	Carnivore	Carnivore	*Felis caracal*	Caracal	Savanna	Kgalagadi National Park	1	I^1	-9.6	-7.6	-6.6	2	13.2	-12.8	-10.8	3.3	-	-	-	-
7737	Carnivore	Carnivore	*Crocuta crocuta*	Spotted hyena	Savanna	Kgalagadi National Park	1	M_1	-8.6	-6.6	-3.7	2	14.3	-10.6	-8.6	2.0	-	-	-	-
7738	Carnivore	Carnivore	*Panthera pardus*	leopard	Savanna	Kgalagadi National Park	1	P4	-9.9	-7.9	-3.1	2	14.5	-11.1	-9.1	1.1	-	-	-	-
7739	Carnivore	Carnivore	*Hyaena brunnea*	brown hyena	Savanna	Kgalagadi National Park	1	M_3	-10.5	-8.5	-3.8	2	15.1	-10.8	-8.8	0.4	-	-	-	-
7740	Carnivore	Carnivore	*Hyaena brunnea*	brown hyena	Savanna	Kgalagadi National Park	1	M_2	-9.2	-7.2	-2.2	2	14.1	-12.2	-10.2	3.0	-	-	-	-
7741	Carnivore	Carnivore	*Hyaena brunnea*	brown hyena	Savanna	Kgalagadi National Park	1	M^2	-7.4	-5.4	0.4	2	14.4	-12.8	-10.8	5.5	-	-	-	-
7742	Carnivore	Carnivore	*Canis mesomelas*	black-backed jackal	Savanna	Kgalagadi National Park	1	M^1	-4.9	-2.9	2.2	2	12.7	-13.3	-11.3	8.4	-	-	-	-
14128	Carnivore	Carnivore	*Panthera pardus*	leopard	Succulent Karoo	Kamieskroon	1	M_1	-8.8	-6.8	2.0	2	15.2	-17.4	-15.4	8.7	-	-	-	-
14352	Primate	Omnivore	*Papio ursinus*	Baboon	Albany Thicket	Graaff Reinet	1	M_1	-6.3	-4.3	-0.6	3	6.1	-11.2	-9.2	4.9	-	-	-	-
14358	Primate	Omnivore	*Papio ursinus*	Baboon	Albany Thicket	Graaff Reinet	1	M_1	-6.9	-4.9	-2.2	3	6.5	-11.8	-9.8	4.8	-	-	-	-
14359	Primate	Omnivore	*Papio ursinus*	Baboon	Albany Thicket	Graaff Reinet	1	M_1	-6.5	-4.5	2.4	2	6.4	-12.9	-10.9	6.4	-	-	-	-
14367	Primate	Omnivore	*Papio ursinus*	Baboon	Albany Thicket	Graaff Reinet	1	M_1	-7.6	-5.6	-2.6	2	6.0	-11.7	-9.7	4.1	-	-	-	-
14369	Primate	Omnivore	*Papio ursinus*	Baboon	Albany Thicket	Graaff Reinet	1	M_1	-6.0	-4.0	1.6	1	5.6	-11.0	-9.0	5.0	-	-	-	-
14371	Primate	Omnivore	*Papio ursinus*	Baboon	Albany Thicket	Graaff Reinet	1	M_1	-6.8	-4.8	2.7	2	6.4	-10.9	-8.9	4.1	-	-	-	-
14373	Primate	Omnivore	*Papio ursinus*	Baboon	Albany Thicket	Graaff Reinet	1	M_1	-7.6	-5.6	1.3	3	6.3	-13.8	-11.8	6.2	-	-	-	-
14375	Primate	Omnivore	*Papio ursinus*	Baboon	Albany Thicket	Graaff Reinet	1	M_1	-5.2	-3.2	1.4	2	5.8	-12.8	-10.8	7.7	-	-	-	-
15340	Primate	Omnivore	*Papio ursinus*	Baboon	Forest	Garden route National Pa	1	M_1	-16.7	-14.7	-4.9	2	4.6	-21.5	-19.5	4.8	-	-	-	-
15341	Primate	Omnivore	*Chlorocebus pygerythrus*	Vervet monkey	Forest	Garden route National Pa	1	M^1	-17.0	-15.0	-4.0	2	4.6	-21.4	-19.4	4.4	-	-	-	-
15345	Primate	Omnivore	*Papio ursinus*	Baboon	Forest	Garden route National Pa	1	M^1	-16.3	-14.3	-3.9	2	3.8	-20.8	-18.8	4.5	-	-	-	-
15350	Primate	Omnivore	*Papio ursinus*	Baboon	Forest	Garden route National Pa	1	M^1	-15.5	-13.5	-1.9	2	5.3	-20.8	-18.8	5.4	-	-	-	-
15355	Primate	Omnivore	*Papio ursinus*	Baboon	Forest	Garden route National Pa	1	M^1	-15.2	-13.2	-3.9	2	7.3	-19.3	-17.3	4.1	-	-	-	-
15357	Primate	Omnivore	*Papio ursinus*	Baboon	Forest	Garden route National Pa	1	M_1	-16.0	-14.0	-1.7	2	4.8	-21.3	-19.3	5.3	-	-	-	-
15358	Primate	Omnivore	*Papio ursinus*	Baboon	Forest	Garden route National Pa	2	-	-15.2	-13.2	-1.8	2	5.9	-20.7	-18.7	5.5	-	-	-	-
15359	Primate	Omnivore	*Papio ursinus*	Baboon	Forest	Garden route National Pa	1	M^2	-14.0	-12.0	-4.1	2	7.2	-19.0	-17.0	5.0	-	-	-	-

APPENDIX 7

$\delta^{13}C$ and $\delta^{18}O$ results from enamel apatite and $\delta^{13}C$ and $\delta^{15}N$ results from bone collagen for all specimens: An average is reported for duplicate results from one individual

UCT	Type	Feeder Type	Species	Common_name	Biome	Location	N Enamel	Tooth sampled	$\delta^{13}C_{enamel}$	Enamel Fossil fuel adjusted	$\delta^{18}O_{enamel}$	N Collagen	$\delta^{15}N_{collagen}$	$\delta^{13}C_{collagen}$	Collagen Fossil fuel adjusted	$\Delta_{enamel-collagen}$	Water behaviour: WD OR WI	Evaporation sensitivity: ES or EI	Size: S, M, L, or Ex L	R or H fermenter
15378	Primate	Omnivore	*Papio ursinus*	Baboon	Forest	Garden route National Pa	1	M^2	-14.5	-12.5	-1.7	2	5.0	-20.5	-18.5	5.9	-	-	-	-
15385	Primate	Omnivore	*Chlorocebus pygerythrus*	Vervet monkey	Forest	Garden route National Pa	1	M_2	-16.0	-14.0	-6.2	2	7.0	-20.3	-18.3	4.3	-	-	-	-
15386	Primate	Omnivore	*Papio ursinus*	Baboon	Forest	Garden route National Pa	1	M_1	-14.9	-12.9	-1.2	2	5.5	-20.9	-18.9	5.9	-	-	-	-
14126	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Sanbona Nature reserve	1	M^1	-12.8	-10.8	1.9						-	-	-	-
14130	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	De hoop	1	M^2	-14.4	-12.4	-1.7						-	-	-	-
14353	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Montague Baths	1	M_1	-15.1	-13.1	0.4	2	5.7	-21.0	-19.0	5.9	-	-	-	-
14354	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Montague Baths	1	M_1	-16.4	-14.4	-0.9	2	6.4	-21.0	-19.0	4.7	-	-	-	-
14355	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Montague Baths	1	M_1	-11.5	-9.5	-1.2	2	6.4	-13.3	-11.3	1.8	-	-	-	-
14356	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Montague Baths	1	M_1	-16.5	-14.5	-0.7	2	5.7	-21.1	-19.1	4.6	-	-	-	-
14357	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Montague Baths	1	M_1	-14.4	-12.4	0.8	2	5.9	-20.7	-18.7	6.4	-	-	-	-
14360	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Montague Baths	1	M_1	-14.8	-12.8	-0.8	2	5.9	-20.3	-18.3	5.5	-	-	-	-
14361	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Montague Baths	1	M_1	-15.2	-13.2	-0.6	2	6.1	-21.2	-19.2	6.0	-	-	-	-
14363	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Montague Baths	1	M_1	-16.7	-14.7	-0.5	2	5.3	-20.6	-18.6	3.9	-	-	-	-
14364	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Montague Baths	1	M_1	-14.7	-12.7	-2.1	2	5.7	-21.0	-19.0	6.3	-	-	-	-
14365	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Montague Baths	1	M_1	-16.0	-14.0	-1.8	2	6.0	-20.6	-18.6	4.7	-	-	-	-
14366	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Montague Baths	1	M_1	-17.1	-15.1	0.1	2	7.1	-20.4	-18.4	3.3	-	-	-	-
14368	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Montague Baths	1	M_1	-14.3	-12.3	0.5	3	6.8	-19.8	-17.8	5.6	-	-	-	-
14370	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Montague Baths	1	M_1	-16.2	-14.2	-4.3	2	5.6	-20.5	-18.5	4.3	-	-	-	-
14372	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Montague Baths	1	M_1	-15.2	-13.2	-0.8	2	5.5	-20.7	-18.7	5.6	-	-	-	-
14374	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Montague Baths	1	M_1	-16.1	-14.1	2.1	2	9.2	-22.0	-20.0	5.9	-	-	-	-
14376	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Montague Baths	1	M_1	-15.5	-13.5	-1.2	2	5.9	-21.1	-19.1	5.5	-	-	-	-
14377	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Montague Baths	1	M_1	-15.6	-13.6	-1.8	2	5.8	-21.1	-19.1	5.5	-	-	-	-
14378	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Montague Baths	1	M_1	-14.6	-12.6	-1.7	2	6.2	-21.0	-19.0	6.4	-	-	-	-
14379	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Montague Baths	1	M_1	-16.2	-14.2	-2.8	2	5.3	-20.6	-18.6	4.4	-	-	-	-
14380	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Montague Baths	1	M_1	-15.6	-13.6	1.9	2	6.2	-20.8	-18.8	5.2	-	-	-	-
15593	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Sandvlakte	1	M_1	-14.3	-12.3	-1.5	2	6.1	-19.0	-17.0	4.7	-	-	-	-
15594	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Sandvlakte	1	M_1	-13.2	-11.2	-2.5	2	5.6	-19.2	-17.2	6.0	-	-	-	-
15595	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Sandvlakte	1	M_1	-13.2	-11.2	-5.1	2	9.6	-17.5	-15.5	4.2	-	-	-	-
15596	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Sandvlakte	1	M^1	-10.7	-8.7	-1.4	2	10.4	-15.4	-13.4	4.7	-	-	-	-
15597	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Sandvlakte	1	M_1	-8.8	-6.8	1.0	2	11.0	-18.6	-16.6	9.8	-	-	-	-
15598	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Sandvlakte	1	M_1	-13.0	-11.0	1.2	2	10.4	-19.0	-17.0	6.0	-	-	-	-
15599	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Sandvlakte	1	M_1	-12.0	-10.0	0.9	2	10.6	-17.2	-15.2	5.2	-	-	-	-
15600	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Sandvlakte	1	M_1	-13.2	-11.2	-5.0	2	10.3	-16.2	-14.2	3.0	-	-	-	-
15601	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Sandvlakte	1	M_1	-12.6	-10.6	-0.4	2	10.7	-18.6	-16.6	6.0	-	-	-	-
15615	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	The Crags, Plett	1	M^2	-14.7	-12.7	-2.9	2	5.8	-20.5	-18.5	5.8	-	-	-	-
15617	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	The Crags, Plett	1	M^1	-15.1	-13.1	-2.0	2	5.7	-20.1	-18.1	5.0	-	-	-	-
15618	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	The Crags, Plett	1	M^1	-15.1	-13.1	-2.6	2	5.0	-20.7	-18.7	5.5	-	-	-	-
15619	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	The Crags, Plett	1	M^1	-14.7	-12.7	-2.2	2	5.2	-20.2	-18.2	5.5	-	-	-	-
15620	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	The Crags, Plett	1	M^1	-14.4	-12.4	-2.3	2	4.8	-19.8	-17.8	5.5	-	-	-	-
15621	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	The Crags, Plett	1	M^1	-14.8	-12.8	-5.6	2	5.8	-19.7	-17.7	4.9	-	-	-	-
15622	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	The Crags, Plett	1	M_1	-15.0	-13.0	-2.9	1	5.2	-21.4	-19.4	6.4	-	-	-	-
15623	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	The Crags, Plett	1	M_1	-15.3	-13.3	-2.9	2	5.5	-20.6	-18.6	5.4	-	-	-	-
15624	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	The Crags, Plett	1	M_1	-14.4	-12.4	-6.5	2	5.4	-20.3	-18.3	5.9	-	-	-	-
15636	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Minwater, oudsthoorn	1	M_1	-13.4	-11.4	2.7	2	7.0	-19.1	-17.1	5.7	-	-	-	-
15637	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Minwater, oudsthoorn	1	M^1	-13.3	-11.3	0.9	2	8.7	-19.3	-17.3	6.0	-	-	-	-
15638	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Minwater, oudsthoorn	1	M_1	-13.7	-11.7	0.5	2	7.9	-18.4	-16.4	4.8	-	-	-	-
15639	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Minwater, oudsthoorn	1	M_1	-13.7	-11.7	1.2	2	9.5	-19.2	-17.2	5.5	-	-	-	-
16061	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Sandvlakte	1	M_1	-12.0	-10.0	-2.6	2	10.1	-18.2	-16.2	6.2	-	-	-	-
16062	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	The Crags, Plett	1	M_1	-15.3	-13.3	-8.9	2	5.3	-20.5	-18.5	5.2	-	-	-	-

APPENDIX 7

$\delta^{13}C$ and $\delta^{18}O$ results from enamel apatite and $\delta^{13}C$ and $\delta^{15}N$ results from bone collagen for all specimens: An average is reported for duplicate results from one individual

UCT	Type	Feeder Type	Species	Common_name	Biome	Location	N Enamel	Tooth sampled	$\delta^{13}C_{enamel}$	Enamel Fossil fuel adjusted	$\delta^{18}O_{enamel}$	N Collagen	$\delta^{15}N_{collagen}$	$\delta^{13}C_{collagen}$	Collagen Fossil fuel adjusted	$\Delta_{enamel-collagen}$	Water behaviour: WD OR WI	Evaporation sensitivity: ES or EI	Size: S, M, L, or Ex L	R or H fermenter
16063	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	The Crags, Plett	1	M_1	-14.9	-12.9	-6.7	2	5.2	-20.6	-18.6	5.7	-	-	-	-
16064	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	The Crags, Plett	1	M_1	-14.9	-12.9	-3.4	2	5.1	-20.1	-18.1	5.3	-	-	-	-
16065	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	The Crags, Plett	1	M_1	-15.0	-13.0	-5.2	2	4.4	-20.5	-18.5	5.6	-	-	-	-
16066	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	The Crags, Plett	1	M_1	-14.9	-12.9	-4.5	2	5.4	-19.5	-17.5	4.7	-	-	-	-
16067	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	The Crags, Plett	1	M_1	-14.1	-12.1	-4.7	2	6.0	-18.9	-16.9	4.8	-	-	-	-
16068	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	The Crags, Plett	1	M_1	-14.8	-12.8	-3.8	2	5.2	-20.2	-18.2	5.5	-	-	-	-
16069	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	The Crags, Plett	1	M_1	-14.8	-12.8	-3.1	2	5.0	-20.3	-18.3	5.5	-	-	-	-
16070	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	The Crags, Plett	1	M_1	-14.1	-12.1	-7.9	2	4.9	-20.2	-18.2	6.2	-	-	-	-
16071	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Sandvlakte	1	M_1	-13.6	-11.6	-2.1	2	6.2	-19.7	-17.7	6.1	-	-	-	-
16072	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	The Crags, Plett	1	M_1	-14.3	-12.3	-2.5	2	4.2	-20.1	-18.1	5.8	-	-	-	-
16073	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	The Crags, Plett	1	M_1	-15.2	-13.2	-3.4	2	4.8	-20.4	-18.4	5.1	-	-	-	-
16074	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Grootkloof, clanwilliam	1	M_1	-15.6	-13.6	0.2	2	9.2	-21.3	-19.3	5.7	-	-	-	-
16075	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Clanwilliam	1	M_1	-14.8	-12.8	-2.9	1	9.4	-21.5	-19.5	6.7	-	-	-	-
16076	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Clanwilliam	1	M_1	-14.7	-12.7	0.5	2	6.0	-21.1	-19.1	6.4	-	-	-	-
16077	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Minwater, oudsthoorn	1	M_1	-14.2	-12.2	2.5	2	9.2	-19.2	-17.2	5.0	-	-	-	-
16078	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Windhoek Bredasdorp	1	M_1	-13.0	-11.0	-3.7	2	5.5	-20.3	-18.3	7.3	-	-	-	-
16079	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Clanwilliam	1	M_1	-13.6	-11.6	-1.2	2	10.1	-15.7	-13.7	2.0	-	-	-	-
16080	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Witpoortdam area, Swart	1	M_1	-12.8	-10.8	1.1	2	10.0	-18.7	-16.7	6.0	-	-	-	-
16081	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Minwater, oudsthoorn	1	M_1	-14.5	-12.5	1.0	2	7.9	-18.6	-16.6	4.1	-	-	-	-
16082	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Minwater, oudsthoorn	1	M_1	-13.1	-11.1	0.8	2	9.8	-18.7	-16.7	5.6	-	-	-	-
16083	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Minwater, oudsthoorn	1	M_1	-12.7	-10.7	2.0	2	8.8	-18.7	-16.7	6.1	-	-	-	-
16084	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Minwater, oudsthoorn	1	M_1	-13.6	-11.6	-9.3	2	8.1	-18.7	-16.7	5.1	-	-	-	-
16155	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Piketberg	1	M_1	-15.1	-13.1	-0.8	2	6.3	-20.9	-18.9	5.8	-	-	-	-
16156	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Piketberg	1	M_1	-15.8	-13.8	0.7	2	6.0	-20.9	-18.9	5.1	-	-	-	-
16157	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Piketberg	1	M_1	-15.3	-13.3	-2.5	2	5.8	-20.7	-18.7	5.4	-	-	-	-
16158	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Piketberg	1	M_1	-14.2	-12.2	0.3	2	5.7	-21.3	-19.3	7.1	-	-	-	-
16159	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Piketberg	1	M_1	-15.9	-13.9	0.9	2	5.7	-21.1	-19.1	5.2	-	-	-	-
16160	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Piketberg	1	M_1	-15.2	-13.2	0.6	2	6.1	-21.3	-19.3	6.1	-	-	-	-
16161	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Piketberg	1	M_1	-15.1	-13.1	1.0	2	6.1	-20.9	-18.9	5.8	-	-	-	-
16162	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Laaiplaas, Robertson	1	M_1	-15.2	-13.2	-3.6	2	4.3	-20.9	-18.9	5.7	-	-	-	-
16163	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Laaiplaas, Robertson	1	M_1	-14.4	-12.4	-0.9	2	4.9	-20.6	-18.6	6.2	-	-	-	-
16164	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Laaiplaas, Robertson	1	M_1	-15.8	-13.8	-0.9	2	4.7	-20.7	-18.7	4.8	-	-	-	-
16165	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Laaiplaas, Robertson	1	M_1	-16.0	-14.0	0.7	2	4.0	-21.3	-19.3	5.2	-	-	-	-
16166	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Laaiplaas, Robertson	1	M_1	-15.9	-13.9	-0.1	2	4.3	-21.2	-19.2	5.3	-	-	-	-
16167	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Laaiplaas, Robertson	1	M_1	-15.5	-13.5	0.1	2	4.4	-21.3	-19.3	5.8	-	-	-	-
16168	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Laaiplaas, Robertson	1	M_1	-15.4	-13.4	-0.1	2	4.4	-21.2	-19.2	5.8	-	-	-	-
16169	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Laaiplaas, Robertson	1	M_1	-15.7	-13.7	-0.9	2	4.1	-21.3	-19.3	5.6	-	-	-	-
16170	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Laaiplaas, Robertson	1	M_1	-15.8	-13.8	-0.8	2	4.4	-21.0	-19.0	5.2	-	-	-	-
16171	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Laaiplaas, Robertson	1	M_1	-16.0	-14.0	-1.1	2	5.7	-20.8	-18.8	4.7	-	-	-	-
16173	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Laaiplaas, Robertson	1	M_1	-15.6	-13.6	0.0	2	4.4	-21.0	-19.0	5.4	-	-	-	-
16174	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Laaiplaas, Robertson	1	M_1	-15.7	-13.7	-1.4	2	4.5	-21.4	-19.4	5.7	-	-	-	-
16175	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Laaiplaas, Robertson	1	M_1	-15.3	-13.3	-0.7	2	5.0	-20.7	-18.7	5.3	-	-	-	-
16176	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Laaiplaas, Robertson	1	M_1	-15.9	-13.9	-0.2	2	4.1	-21.1	-19.1	5.2	-	-	-	-
16177	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Laaiplaas, Robertson	1	M_1	-15.4	-13.4	-0.4	2	3.5	-21.2	-19.2	5.9	-	-	-	-
16178	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Laaiplaas, Robertson	1	M_1	-16.0	-14.0	-0.1	2	4.0	-21.2	-19.2	5.2	-	-	-	-
16179	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Laaiplaas, Robertson	1	M_1	-15.6	-13.6	0.4	2	3.9	-21.3	-19.3	5.7	-	-	-	-
16180	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Laaiplaas, Robertson	1	M_1	-14.9	-12.9	-1.2	2	6.8	-18.7	-16.7	3.8	-	-	-	-
16201	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Grootvadersbosch	1	M_1	-16.8	-14.8	-1.8	2	4.3	-20.9	-18.9	4.2	-	-	-	-
16203	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Reiersvlei	1	M^1	-12.7	-10.7	-0.5	2	8.6	-17.9	-15.9	5.1	-	-	-	-

APPENDIX 7

$\delta^{13}C$ and $\delta^{18}O$ results from enamel apatite and $\delta^{13}C$ and $\delta^{15}N$ results from bone collagen for all specimens: An average is reported for duplicate results from one individual

UCT	Type	Feeder Type	Species	Common_name	Biome	Location	N Enamel	Tooth sampled	$\delta^{13}C_{enamel}$	Enamel Fossil fuel adjusted	$\delta^{18}O_{enamel}$	N Collagen	$\delta^{15}N_{collagen}$	$\delta^{13}C_{collagen}$	Collagen Fossil fuel adjusted	$\Delta_{enamel-collagen}$	Water behaviour: WD OR WI	Evaporation sensitivity: ES or EI	Size: S, M, L, or Ex L	R or H ferment
16204	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Swellendam	1	M_1	-13.1	-11.1	-1.3	2	7.6	-19.2	-17.2	6.1	-	-	-	-
16205	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Swellendam	1	M_1	-13.3	-11.3	-0.5	2	7.5	-19.7	-17.7	6.4	-	-	-	-
16206	Primate	Omnivore	*Papio ursinus*	Baboon	Fynbos	Swellendam	1	M_1	-12.7	-10.7	0.8	2	7.6	-19.2	-17.2	6.5	-	-	-	-
15640	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M^1	-13.2	-11.2	0.8	2	6.5	-19.5	-17.5	6.3	-	-	-	-
15641	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M^1	-13.9	-11.9	1.2	2	6.1	-19.3	-17.3	5.3	-	-	-	-
15642	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M^1	-13.8	-11.8	-2.6	2	7.6	-19.8	-17.8	6.0	-	-	-	-
15643	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M^1	-14.7	-12.7	2.1	2	7.4	-19.9	-17.9	5.2	-	-	-	-
15644	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M^1	-13.4	-11.4	1.7	2	8.2	-20.3	-18.3	6.9	-	-	-	-
15645	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M_1	-13.7	-11.7	2.1	2	6.7	-19.6	-17.6	5.9	-	-	-	-
15646	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M_1	-14.4	-12.4	-0.3	2	7.4	-19.6	-17.6	5.3	-	-	-	-
15647	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M^1	-13.6	-11.6	1.2	2	6.8	-19.6	-17.6	5.9	-	-	-	-
16181	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M^1	-13.7	-11.7	1.5	2	7.6	-19.3	-17.3	5.5	-	-	-	-
16182	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M^1	-13.7	-11.7	1.7	2	6.1	-19.6	-17.6	5.9	-	-	-	-
16183	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M^1	-13.0	-11.0	0.7	2	6.7	-19.9	-17.9	6.9	-	-	-	-
16184	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M_1	-12.0	-10.0	2.1	2	14.3	-18.3	-16.3	6.2	-	-	-	-
16185	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M_1	-13.9	-11.9	1.3	2	7.0	-19.4	-17.4	5.6	-	-	-	-
16186	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M^1	-14.1	-12.1	1.6	2	6.6	-19.8	-17.8	5.7	-	-	-	-
16187	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M_1	-13.5	-11.5	2.2	2	6.8	-19.5	-17.5	5.9	-	-	-	-
16188	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M^1	-15.1	-13.1	0.1	2	6.2	-19.6	-17.6	4.4	-	-	-	-
16189	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M_1	-5.2	-3.2	1.3	2	7.3	-19.2	-17.2	14.0	-	-	-	-
16190	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M_1	-14.7	-12.7	2.5	2	6.7	-21.2	-19.2	6.6	-	-	-	-
16191	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M^1	-13.1	-11.1	2.2	2	7.3	-19.6	-17.6	6.5	-	-	-	-
16192	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M^1	-15.0	-13.0	-0.1	2	7.1	-19.6	-17.6	4.6	-	-	-	-
16193	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M_1	-13.9	-11.9	-4.7	2	7.4	-19.9	-17.9	6.0	-	-	-	-
16194	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M^1	-13.7	-11.7	2.5	2	7.2	-19.4	-17.4	5.7	-	-	-	-
16195	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M^1	-13.4	-11.4	0.6	2	10.6	-19.2	-17.2	5.8	-	-	-	-
16196	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M^1	-13.4	-11.4	1.6	2	8.0	-19.5	-17.5	6.1	-	-	-	-
16197	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M_1	-13.7	-11.7	-0.1	2	7.5	-19.5	-17.5	5.8	-	-	-	-
16198	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M_1	-14.3	-12.3	0.3	2	8.6	-20.2	-18.2	5.9	-	-	-	-
16199	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M_1	-13.1	-11.1	1.5	2	7.2	-19.6	-17.6	6.5	-	-	-	-
16200	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Laingsburg	1	M_1	-13.7	-11.7	-3.4	2	6.5	-19.9	-17.9	6.3	-	-	-	-
16202	Primate	Omnivore	*Papio ursinus*	Baboon	Succulent Karoo	Willowmore	1	M_1	-13.8	-11.8	2.5	2	10.4	-18.7	-16.7	4.9	-	-	-	-
1701	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	1	M	-5.2	-3.2	2.3						WD	EI	L	R
1702	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	2	-	-4.5	-2.5	1.3	2	12.2	-13.9	-11.9	9.4	WD	EI	L	R
1703	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	1	M	-1.4	0.6	1.1						WD	EI	L	R
1704	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	1	M	-5.7	-3.7	-5.1						WD	EI	L	R
1705	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	1	M	-5.8	-3.8	-0.3						WD	EI	L	R
1706	Ungulate	Browser	*Taurotragus oryx*	Eland	Albany Thicket	Addo national Park	1	M	-8.8	-6.8	1.4						WI	ES	L	R
1707	Ungulate	Browser	*Taurotragus oryx*	Eland	Albany Thicket	Addo national Park	1	M	-8.1	-6.1	3.6						WI	ES	L	R
1708	Ungulate	Browser	*Taurotragus oryx*	Eland	Albany Thicket	Addo national Park	2	-	-9.5	-7.5	1.7	2	9.3	-17.6	-15.6	8.1	WI	ES	L	R
1709	Ungulate	Browser	*Tragelaphus strepsiceros*	Kudu	Albany Thicket	Addo national Park	4	-	-10.3	-8.3	2.1	2	12.8	-16.9	-14.9	6.6	WD	ES	L	R
1710	Ungulate	Browser	*Tragelaphus strepsiceros*	Kudu	Albany Thicket	Addo national Park	5	-	-10.9	-8.9	1.5	2	12.5	-16.6	-14.6	5.6	WD	ES	L	R
1711	Ungulate	Browser	*Tragelaphus strepsiceros*	Kudu	Albany Thicket	Addo national Park	4	-	-11.2	-9.2	1.8	2	12.4	-16.6	-14.6	5.4	WD	ES	L	R
2637	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	3	-	-3.6	-1.6	0.8	3	12.3	-14.2	-12.2	10.6	WD	EI	L	R
2638	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	1	M2	-3.2	-1.2	2.0	2	13.5	-16.0	-14.0	12.8	WD	EI	L	R
2639	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	2	-	-2.9	-0.9	0.2						WD	EI	L	R
2640	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	1	M3	-3.1	-1.1	1.1	2	11.9	-12.8	-10.8	9.6	WD	EI	L	R
2641	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	1	M3	-4.4	-2.4	1.9	2	12.4	-13.8	-11.8	9.4	WD	EI	L	R
2643	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	1	M3	-2.5	-0.5	1.1	2	12.4	-13.8	-11.8	11.3	WD	EI	L	R

APPENDIX 7

$\delta^{13}C$ and $\delta^{18}O$ results from enamel apatite and $\delta^{13}C$ and $\delta^{15}N$ results from bone collagen for all specimens: An average is reported for duplicate results from one individual

UCT	Type	Feeder Type	Species	Common_name	Biome	Location	N Enamel	Tooth sampled	$\delta^{13}C_{enamel}$	Enamel Fossil fuel adjusted	$\delta^{18}O_{enamel}$	N Collagen	$\delta^{15}N_{collagen}$	$\delta^{13}C_{collagen}$	Collagen Fossil fuel adjusted	$\Delta_{enamel-collagen}$	Water behaviour: WD OR WI	Evaporation sensitivity: ES or EI	Size: S, M, L, or Ex L	R or H fermenter
2645	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	1	M3	-4.9	-2.9	1.3	2	12.4	-13.2	-11.2	8.4	WD	EI	L	R
2646	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	1	M3	-3.2	-1.2	0.1	2	12.3	-13.9	-11.9	10.6	WD	EI	L	R
2647	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	1	M3	-3.3	-1.3	0.2	2	12.4	-13.1	-11.1	9.8	WD	EI	L	R
2648	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	1	M3	-0.8	1.2	1.3	2	11.8	-14.0	-12.0	13.3	WD	EI	L	R
2649	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	1	M3	-4.8	-2.8	0.5	2	10.4	-12.2	-10.2	7.5	WD	EI	L	R
2650	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	1	M3	-2.1	-0.1	-0.4	2	13.0	-14.6	-12.6	12.5	WD	EI	L	R
2651	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	2	-	-4.3	-2.3	-0.8	2	12.5	-12.3	-10.3	8.0	WD	EI	L	R
2659	Ungulate	Browser	*Taurotragus oryx*	Eland	Albany Thicket	Addo national Park	1	M2	-9.9	-7.9	1.2	2	8.7	-18.1	-16.1	8.2	WI	ES	L	R
2660	Ungulate	Browser	*Taurotragus oryx*	Eland	Albany Thicket	Addo national Park	1	M3	-8.9	-6.9	1.7	2	10.1	-17.3	-15.3	8.3	WI	ES	L	R
14015	Ungulate	Browser	*Tragelaphus scriptus*	Bushbuck	Albany Thicket	Thyspunt, Jeffreys Bay	1	M_1	-9.2	-7.2	-0.2						WD	ES	M	R
14285	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Albany Thicket	Addo national Park	1	M_1	-3.5	-1.5	-6.7	2	10.6	-8.2	-6.2	4.7	WI	EI	L	R
14286	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	1	M^1	-3.2	-1.2	-1.4	2	11.8	-11.9	-9.9	8.7	WD	EI	L	R
14287	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	1	M^1	-1.5	0.5	-2.1	2	10.0	-10.5	-8.5	9.0	WD	EI	L	R
14288	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	1	M^1	-1.7	0.3	0.1	2	8.9	-9.2	-7.2	7.5	WD	EI	L	R
14289	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	1	M^1	-6.0	-4.0	0.5	2	12.9	-13.2	-11.2	7.3	WD	EI	L	R
14290	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	1	M^1	-3.1	-1.1	-3.6	3	11.1	-11.8	-9.8	8.7	WD	EI	L	R
14291	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	1	M_1	-4.0	-2.0	0.2	2	13.2	-10.3	-8.3	6.3	WD	EI	L	R
14292	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Albany Thicket	Addo national Park	1	M_1	-1.0	1.0	-0.2	2	9.6	-9.5	-7.5	8.6	WI	EI	L	R
14293	Ungulate	Browser	*Tragelaphus strepsiceros*	Kudu	Albany Thicket	Addo national Park	1	M_1	-12.6	-10.6	1.5	2	12.2	-19.7	-17.7	7.1	WD	ES	L	R
14294	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Albany Thicket	Addo national Park	1	M^1	-3.1	-1.1	0.0	2	10.8	-8.7	-6.7	5.7	WI	EI	L	R
14295	Ungulate	Grazer	*Phacochoerus africanus*	Warthog	Albany Thicket	Addo national Park	1	M^1	-7.7	-5.7	-9.1	2	12.5	-11.6	-9.6	4.0	WI	EI	M	H
14296	Ungulate	Grazer	*Phacochoerus africanus*	Warthog	Albany Thicket	Addo national Park	1	M^1	-6.5	-4.5	-5.2	2	12.7	-10.9	-8.9	4.3	WI	EI	M	H
14297	Ungulate	Grazer	*Phacochoerus africanus*	Warthog	Albany Thicket	Addo national Park	1	M^2	-5.6	-3.6	-4.9	2	10.3	-12.6	-10.6	6.9	WI	EI	M	H
14300	Ungulate	Grazer	*Phacochoerus africanus*	Warthog	Albany Thicket	Addo national Park	1	M^2	-10.7	-8.7	-1.3	2	9.5	-17.5	-15.5	6.8	WI	EI	M	H
14301	Ungulate	Grazer	*Phacochoerus africanus*	Warthog	Albany Thicket	Addo national Park	1	M_3	-7.0	-5.0	-4.8	2	9.1	-12.5	-10.5	5.6	WI	EI	M	H
14302	Ungulate	Grazer	*Phacochoerus africanus*	Warthog	Albany Thicket	Addo national Park	1	M^2	-5.7	-3.7	-3.6	2	11.7	-12.0	-10.0	6.4	WI	EI	M	H
14303	Ungulate	Grazer	*Phacochoerus africanus*	Warthog	Albany Thicket	Addo national Park	1	M^3	-5.7	-3.7	-5.8	2	10.3	-10.9	-8.9	5.2	WI	EI	M	H
14304	Ungulate	Browser	*Tragelaphus strepsiceros*	Kudu	Albany Thicket	Addo national Park	1	M^2	-14.2	-12.2	1.0	2	8.2	-21.0	-19.0	6.8	WD	ES	L	R
14305	Ungulate	Browser	*Tragelaphus strepsiceros*	Kudu	Albany Thicket	Addo national Park	1	M^1	-15.0	-13.0	1.3	2	13.3	-16.6	-14.6	1.7	WD	ES	L	R
14309	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	1	M^1	-0.7	1.3	0.5	2	10.9	-9.2	-7.2	8.6	WD	EI	L	R
14310	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Albany Thicket	Addo national Park	1	M^1	0.7	2.7	3.4	2	11.0	-9.3	-7.3	9.9	WD	EI	L	R
14311	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Albany Thicket	Addo national Park	1	M^1	-1.4	0.6	-4.7	2	10.8	-6.9	-4.9	5.5	WI	EI	L	R
14312	Ungulate	Browser	*Taurotragus oryx*	Eland	Albany Thicket	Addo national Park	1	M^1	-9.9	-7.9	0.3	2	12.0	-15.1	-13.1	5.2	WI	ES	L	R
14313	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Albany Thicket	Addo national Park	1	M^1	0.1	2.1	0.9	2	10.7	-7.9	-5.9	8.0	WI	EI	L	R
14314	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Albany Thicket	Addo national Park	1	M^1	0.0	2.0	-0.4	2	12.0	-7.6	-5.6	7.6	WI	EI	L	R
14315	Ungulate	Browser	*Tragelaphus strepsiceros*	Kudu	Albany Thicket	Addo national Park	1	M^1	-14.5	-12.5	1.7	2	11.9	-19.7	-17.7	5.2	WD	ES	L	R
14316	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Albany Thicket	Addo national Park	1	M^1	0.3	2.3	0.5	2	10.7	-8.4	-6.4	8.7	WI	EI	L	R
14317	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Albany Thicket	Addo national Park	1	M^1	-1.4	0.6	2.1	2	12.4	-10.0	-8.0	8.6	WI	EI	L	R
14318	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Albany Thicket	Addo national Park	1	M^1	0.9	2.9	0.7	2	10.5	-7.7	-5.7	8.6	WI	EI	L	R
14319	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Albany Thicket	Addo national Park	1	M^3	1.6	3.6	0.0	2	12.2	-8.0	-6.0	9.6	WI	EI	L	R
14320	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Albany Thicket	Addo national Park	1	M^1	-0.7	1.3	0.0	2	11.1	-8.0	-6.0	7.4	WI	EI	L	R
14321	Ungulate	Browser	*Tragelaphus strepsiceros*	Kudu	Albany Thicket	Addo national Park	1	M^1	-13.3	-11.3	-0.3	2	11.0	-20.5	-18.5	7.2	WD	ES	L	R
14322	Ungulate	Browser	*Tragelaphus scriptus*	Bushbuck	Albany Thicket	Addo national Park	1	M^1	-15.0	-13.0	-5.5	2	11.6	-19.4	-17.4	4.4	WD	ES	M	R
14323	Ungulate	Browser	*Tragelaphus scriptus*	Bushbuck	Albany Thicket	Addo national Park	1	M^1	-16.0	-14.0	-2.9	2	10.6	-19.1	-17.1	3.1	WD	ES	M	R
14324	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Albany Thicket	Addo national Park	1	M^1	-0.7	1.3	-1.0	2	11.7	-8.2	-6.2	7.5	WI	EI	L	R
14325	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Albany Thicket	Addo national Park	1	M^1	0.4	2.4	-0.8	5	11.1	-8.5	-6.5	8.9	WI	EI	L	R
14326	Ungulate	Browser	*Tragelaphus strepsiceros*	Kudu	Albany Thicket	Addo national Park	1	M^1	-14.1	-12.1	0.8	2	11.2	-21.1	-19.1	7.0	WD	ES	L	R
15430	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Albany Thicket	Addo national Park	1	M_1	-0.5	1.5	-0.4	2	11.2	-8.1	-6.1	7.6	WI	EI	L	R
15431	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Albany Thicket	Addo national Park	1	M_1	-1.6	0.4	-10.8	2	11.5	-8.8	-6.8	7.2	WI	EI	L	R

APPENDIX 7

$\delta^{13}C$ and $\delta^{18}O$ results from enamel apatite and $\delta^{13}C$ and $\delta^{15}N$ results from bone collagen for all specimens: An average is reported for duplicate results from one individual

UCT	Type	Feeder Type	Species	Common_name	Biome	Location	N Enamel	Tooth sampled	$\delta^{13}C_{enamel}$	Enamel Fossil fuel adjusted	$\delta^{18}O_{enamel}$	N Collagen	$\delta^{15}N_{collagen}$	$\delta^{13}C_{collagen}$	Collagen Fossil fuel adjusted	$\Delta_{enamel-collagen}$	Water behaviour: WD OR WI	Evaporation sensitivity: ES or EI	Size: S, M, L, or Ex L	R or H fermenter
15432	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Albany Thicket	Addo national Park	1	M_1	-0.3	1.7	-0.4	2	10.5	-9.2	-7.2	8.9	WI	EI	L	R
15433	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Albany Thicket	Addo national Park	1	M_1	2.0	4.0	-0.6	2	11.2	-7.8	-5.8	9.8	WI	EI	L	R
15435	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Albany Thicket	Addo national Park	1	M_1	1.6	3.6	-4.2	2	10.7	-7.4	-5.4	9.0	WI	EI	L	R
15436	Ungulate	Browser	*Taurotragus oryx*	Eland	Albany Thicket	Addo national Park	1	M_1	-11.9	-9.9	1.6						WI	ES	L	R
15437	Ungulate	Browser	*Taurotragus oryx*	Eland	Albany Thicket	Addo national Park	1	M_1	-12.2	-10.2	-3.7	2	11.8	-19.9	-17.9	7.7	WI	ES	L	R
15438	Ungulate	Browser	*Taurotragus oryx*	Eland	Albany Thicket	Addo national Park	1	M_1	-12.6	-10.6	-1.1	2	10.8	-20.1	-18.1	7.5	WI	ES	L	R
15439	Ungulate	Grazer	*Redunca arundinum*	Southern reedbuck	Albany Thicket	Addo national Park	1	M_1	-0.2	1.8	-6.3	2	4.7	-7.5	-5.5	7.3	WD	EI	M	R
15440	Ungulate	Browser	*Tragelaphus scriptus*	Bushbuck	Albany Thicket	Addo national Park	1	M_1	-18.1	-16.1	-0.6	2	10.7	-22.6	-20.6	4.6	WD	ES	M	R
1667	Ungulate	Browser	*Cephalophus monticola*	Blue duiker	Forest	Knysna	5	-	-14.2	-12.2	-4.6	2	4.3	-22.4	-20.4	8.3	WI	ES	S	R
1670	Ungulate	Omnivore	*Potamochoerus larvatus*	Bushpig	Forest	Knysna	6	-	-14.1	-12.1	-4.9	2	7.9	-20.4	-18.4	6.3	WD	EI	M	H
15332	Ungulate	Omnivore	*Potamochoerus larvatus*	Bushpig	Forest	Garden route National Pa	3	-	-15.4	-13.4	-4.9	2	6.8	-21.4	-19.4	6.0	WD	EI	M	H
15333	Ungulate	Browser	*Tragelaphus scriptus*	Bushbuck	Forest	Garden route National Pa	1	M^1	-18.1	-16.1	-5.6	2	3.9	-23.5	-21.5	5.4	WD	ES	M	R
15334	Ungulate	Browser	*Tragelaphus scriptus*	Bushbuck	Forest	Garden route National Pa	1	M^1	-17.9	-15.9	-9.2	2	3.2	-24.8	-22.8	6.8	WD	ES	M	R
15335	Ungulate	Browser	*Tragelaphus scriptus*	Bushbuck	Forest	Garden route National Pa	1	M^1	-18.5	-16.5	-8.4	2	3.1	-23.5	-21.5	5.0	WD	ES	M	R
15336	Ungulate	Browser	*Raphicerus sp*	Steenbok/Grysbok	Forest	Garden route National Pa	1	M_1	-15.3	-13.3	-5.9	2	10.7	-20.1	-18.1	4.8	WI	ES	S	R
15337	Ungulate	Omnivore	*Potamochoerus larvatus*	Bushpig	Forest	Garden route National Pa	1	P_4	-14.4	-12.4	-4.7	2	8.7	-19.0	-17.0	4.5	WD	EI	M	H
15338	Ungulate	Omnivore	*Potamochoerus larvatus*	Bushpig	Forest	Garden route National Pa	3	-	-16.6	-14.6	-5.6	2	4.6	-20.6	-18.6	4.0	WD	EI	M	H
15339	Ungulate	Omnivore	*Potamochoerus larvatus*	Bushpig	Forest	Garden route National Pa	1	M_1	-17.5	-15.5	-11.3	2	5.8	-20.8	-18.8	3.2	WD	EI	M	H
15343	Ungulate	Omnivore	*Potamochoerus larvatus*	Bushpig	Forest	Garden route National Pa	1	M^1	-15.4	-13.4	-5.5	2	8.1	-21.0	-19.0	5.6	WD	EI	M	H
15347	Ungulate	Omnivore	*Potamochoerus larvatus*	Bushpig	Forest	Garden route National Pa	1	M_1	-14.6	-12.6	-8.7	2	5.8	-20.5	-18.5	6.0	WD	EI	M	H
15348	Ungulate	Omnivore	*Potamochoerus larvatus*	Bushpig	Forest	Garden route National Pa	2	-	-15.1	-13.1	-5.1	2	5.8	-22.1	-20.1	7.0	WD	EI	M	H
15349	Ungulate	Omnivore	*Potamochoerus larvatus*	Bushpig	Forest	Garden route National Pa	1	M_3	-14.2	-12.2	-6.1	2	6.3	-22.8	-20.8	8.7	WD	EI	M	H
15351	Ungulate	Browser	*Loxodonta africana*	Elephant	Forest	Garden route National Pa	1	M	-13.4	-11.4	-3.9						WD	EI	Ex L	H
15352	Ungulate	Browser	*Raphicerus melanotis*	Grysbok	Forest	Garden route National Pa	1	M_1	-16.7	-14.7	-5.8	2	3.6	-22.2	-20.2	5.6	WI	ES	S	R
15353	Ungulate	Browser	*Raphicerus melanotis*	Grysbok	Forest	Garden route National Pa	1	M^1	-15.5	-13.5	-5.7	2	3.2	-21.8	-19.8	6.3	WI	ES	S	R
15354	Ungulate	Browser	*Raphicerus melanotis*	Grysbok	Forest	Garden route National Pa	1	M^1	-15.1	-13.1	-8.6	2	5.5	-21.6	-19.6	6.6	WI	ES	S	R
15360	Ungulate	Browser	*Cephalophus monticola*	Blue duiker	Forest	Garden route National Pa	1	-				2	5.1	-21.8	-19.8		WI	ES	S	R
15365	Ungulate	Grazer	*Hippopotamus amphibius*	Hippopotamus	Forest	Garden route National Pa	1	-				2	11.0	-16.6	-14.6		WD	EI	Ex L	R
15366	Ungulate	Browser	*Tragelaphus scriptus*	Bushbuck	Forest	Garden route National Pa	1	M^2	-15.4	-13.4	-8.8	2	6.0	-22.0	-20.0	6.6	WD	ES	M	R
15367	Ungulate	Omnivore	*Potamochoerus larvatus*	Bushpig	Forest	Garden route National Pa	1	M_1	-14.2	-12.2	-5.2	2	4.4	-20.5	-18.5	6.3	WD	EI	M	H
15368	Ungulate	Omnivore	*Potamochoerus larvatus*	Bushpig	Forest	Garden route National Pa	1	M_1	-15.1	-13.1	-7.3	2	6.1	-19.8	-17.8	4.8	WD	EI	M	H
15370	Ungulate	Browser	*Taurotragus oryx*	Eland	Forest	Garden route National Park		-				2	3.3	-19.8	-17.8		WI	ES	L	R
15371	Ungulate	Browser	*Taurotragus oryx*	Eland	Forest	Garden route National Park		-				2	7.9	-20.9	-18.9		WI	ES	L	R
15372	Ungulate	Grazer	*Hippopotamus amphibius*	Hippopotamus	Forest	Garden route National Pa	1	-				2	5.0	-9.7	-7.7		WD	EI	Ex L	R
15373	Ungulate	Grazer	*Hippopotamus amphibius*	Hippopotamus	Forest	Garden route National Pa	1	-				2	6.6	-11.8	-9.8		WD	EI	Ex L	R
15374	Ungulate	Grazer	*Syncerus caffer*	Buffalo	Forest	Garden route National Park		-				2	11.9	-9.7	-7.7		WD	EI	L	R
15375	Ungulate	Omnivore	*Potamochoerus larvatus*	Bushpig	Forest	Garden route National Pa	3	-	-14.0	-12.0	-6.1	2	6.6	-21.1	-19.1	7.1	WD	EI	M	H
15376	Ungulate	Browser	*Taurotragus oryx*	Eland	Forest	Garden route National Park		-				2	2.9	-19.6	-17.6		WI	ES	L	R
15379	Ungulate	Omnivore	*Potamochoerus larvatus*	Bushpig	Forest	Garden route National Pa	2	-	-15.2	-13.2	-3.9	2	7.8	-21.9	-19.9	6.8	WD	EI	M	H
15381	Ungulate	Browser	*Tragelaphus scriptus*	Bushbuck	Forest	Garden route National Park		-				2	3.6	-23.0	-21.0		WD	ES	M	R
15382	Ungulate	Browser	*Tragelaphus scriptus*	Bushbuck	Forest	Garden route National Park		-				2	5.2	-22.8	-20.8		WD	ES	M	R
15384	Ungulate	Browser	*Cephalophus monticola*	Blue duiker	Forest	Garden route National Pa	1	M_2	-14.3	-12.3	-7.8	2	3.5	-21.1	-19.1	6.9	WI	ES	S	R
1074	Ungulate	Browser	*Raphicerus campestris*	Steenbok	Fynbos	Kruisfontein, EB	5	-	-13.6	-11.6	4.8	2	11.1	-19.3	-17.3	5.7	WI	ES	S	R
2063	Ungulate	Grazer	*Damaliscus pygargus pyga*	Bontebok	Fynbos	Cape Point Nature reserve		-				2	5.4	-20.8	-18.8		WD	EI	M	R
2066	Ungulate	Browser	*Raphicerus campestris*	Steenbok	Fynbos	Elands Bay	6	-	-13.2	-11.2	4.7	2	14.1	-20.1	-18.1	6.9	WI	ES	S	R
2067	Ungulate	Browser	*Raphicerus campestris*	Steenbok	Fynbos	Elands Bay	3	-	-13.4	-11.4	4.3	2	13.2	-20.1	-18.1	6.7	WI	ES	S	R
2073	Ungulate	Browser	*Raphicerus campestris*	Steenbok	Fynbos	Ysterfontein	5	-	-11.2	-9.2	1.8	2	7.2	-19.8	-17.8	8.7	WI	ES	S	R
2080	Ungulate	Browser	*Raphicerus melanotis*	Grysbok	Fynbos	Byneskranskop, Die keld	3	-	-14.9	-12.9	-2.0	2	5.5	-21.8	-19.8	6.9	WI	ES	S	R
2111	Ungulate	Browser	*Raphicerus melanotis*	Grysbok	Fynbos	Cederberg	3	-	-14.1	-12.1	2.3	2	5.6	-21.1	-19.1	7.0	WI	ES	S	R

APPENDIX 7

$\delta^{13}C$ and $\delta^{18}O$ results from enamel apatite and $\delta^{13}C$ and $\delta^{15}N$ results from bone collagen for all specimens: An average is reported for duplicate results from one individual

UCT	Type	Feeder Type	Species	Common_name	Biome	Location	N Enamel	Tooth sampled	$\delta^{13}C_{enamel}$	Enamel Fossil fuel adjusted	$\delta^{18}O_{enamel}$	N Collagen	$\delta^{15}N_{collagen}$	$\delta^{13}C_{collagen}$	Collagen Fossil fuel adjusted	$\Delta_{enamel-collagen}$	Water behaviour: WD OR WI	Evaporation sensitivity: ES or EI	Size: S, M, L, or Ex L	R or H fermenter
13958	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Fynbos	Ikwa ttu, western cape	5	-	-15.6	-13.6	0.2	2	3.5	-22.2	-20.2	6.6	WI	ES	S	R
13973	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Fynbos	Elandsfontein, western ca	1	M_1	-16.0	-14.0	2.6	2	3.9	-21.3	-19.3	5.3	WI	ES	S	R
13977	Ungulate	Browser	*Raphicerus melanotis*	Grysbok	Fynbos	Blombos	1	M^1	-15.6	-13.6	0.0	2	1.8	-20.9	-18.9	5.3	WI	ES	S	R
13978	Ungulate	Browser	*Oreotragus oreotragus*	Klipspringer	Fynbos	Cederberg	1	M_1	-15.3	-13.3	8.5	2	16.1	-21.2	-19.2	5.9	WI	ES	S	R
14009	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Fynbos	Koeberg Nature Resserv	1	M_1	-15.3	-13.3	-2.2	2	4.3	-21.1	-19.1	5.9	WI	ES	S	R
14012	Ungulate	Grazer	*Equus zebra*	Mountain zebra	Fynbos	De Hoop	1	M_1	-10.0	-8.0	-5.2						WD	EI	L	H
14032	Ungulate	Grazer	*Damaliscus pygargus pyga*	Bontebok	Fynbos	Bontebok National Park	1	M_1	-7.7	-5.7	-2.6	2	7.7	-15.2	-13.2	7.5	WD	EI	M	R
14033	Ungulate	Browser	*Pelea capreolus*	Grey rhebuck	Fynbos	Bontebok National Park	1	M_1	-18.9	-16.9	-3.0	2	6.9	-21.5	-19.5	2.6	WI	ES	S	R
14042	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Fynbos	Koeberg Nat. Res.	1	M^1	-14.4	-12.4	0.3						WI	ES	S	R
14043	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Fynbos	Vrolikheid Nature reserve	1	M_1	-14.0	-12.0	1.2						WI	ES	S	R
14048	Ungulate	Browser	*Oreotragus oreotragus*	Klipspringer	Fynbos	Diepkloof, cerderberg	1	M_1	-8.8	-6.8	3.1						WI	ES	S	R
14049	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Fynbos	Lamberts Bay	1	M_1	-12.9	-10.9	2.4						WI	ES	S	R
14050	Ungulate	Browser	*Raphicerus melanotis*	Grysbok	Fynbos	De Mond	1	M_1	-11.8	-9.8	-1.2						WI	ES	S	R
14051	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Fynbos	De Hoop	1	M_1	-15.0	-13.0	-0.2						WI	ES	S	R
14052	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Fynbos	Lamberts Bay	1	M_1	-13.5	-11.5	1.7						WI	ES	S	R
14053	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Fynbos	Velddrift	1	M_1	-13.7	-11.7	0.9						WI	ES	S	R
14054	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Fynbos	Lamberts Bay	1	M_1	-13.3	-11.3	0.4						WI	ES	S	R
14055	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Fynbos	De Hoop	1	M_1	-14.4	-12.4	0.2						WI	ES	S	R
14133	Ungulate	Browser	*Raphicerus melanotis*	Grysbok	Fynbos	Somerset west	1	M^3	-15.9	-13.9	-2.0						WI	ES	S	R
14137	Ungulate	Omnivore	*Potamochoerus larvatus*	Bushpig	Fynbos	bredasdorp	5	-	-8.9	-6.9	-3.1						WD	EI	M	H
14696	Ungulate	Browser	*Raphicerus melanotis*	Grysbok	Fynbos	Koeberg Nat. Res.	1	M_2				2	5.4	-20.7	-18.7		WI	ES	S	R
16370	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Fynbos	Bontebok National Park	3	-	-5.1	-3.1	-1.7	2	6.5	-13.3	-11.3	8.2	WI	EI	L	R
16371	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Fynbos	West Coast National Park		-				2	10.0	-20.0	-18.0		WI	EI	L	R
16373	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Fynbos	West Coast National Park		-				2	11.1	-20.4	-18.4		WI	EI	L	R
16374	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Fynbos	West Coast National Park		-				2	11.5	-20.8	-18.8		WI	EI	L	R
16375	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Fynbos	West Coast National Park		-				2	9.6	-21.4	-19.4		WI	EI	L	R
16376	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Fynbos	West Coast National Park		-				2	10.9	-17.9	-15.9		WI	EI	L	R
16377	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Fynbos	West Coast National Park		-				2	13.7	-19.7	-17.7		WI	EI	L	R
16378	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Fynbos	West Coast National Park		-				2	11.6	-18.3	-16.3		WI	EI	L	R
16379	Ungulate	Grazer	*Alcelaphine*	Bonetbok/Hartebeest	Fynbos	West Coast National Park		-				2	10.4	-21.1	-19.1		WI	EI	L	R
16381	Ungulate	Grazer	*Alcelaphine*	Bonetbok/Hartebeest	Fynbos	West Coast National Park		-				2	10.2	-21.5	-19.5		WI	EI	L	R
16382	Ungulate	Grazer	*Alcelaphine*	Bonetbok/Hartebeest	Fynbos	West Coast National Park		-				2	8.9	-22.4	-20.4		WI	EI	L	R
16383	Ungulate	Grazer	*Alcelaphine*	Bonetbok/Hartebeest	Fynbos	West Coast National Park		-				2	11.4	-18.9	-16.9		WI	EI	L	R
16384	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Fynbos	West Coast National Parl	3	-	-14.5	-12.5	2.1	2	6.2	-21.5	-19.5	7.0	WI	ES	S	R
2130	Ungulate	Browser	*Raphicerus campestris*	Steenbok	Nama Karoo	Boesmansberg	5	-	-9.9	-7.9	8.8	2	13.0	-17.3	-15.3	7.4	WI	ES	S	R
3933	Ungulate	Browser	*Raphicerus campestris*	Steenbok	Nama Karoo	Jagtpan, Karoo		-				2	10.1	-18.8	-16.8		WI	ES	S	R
8080	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Nama Karoo	Karoo National Park	5	-	-10.9	-8.9	4.5	2	11.9	-20.0	-18.0	9.1	WI	ES	M	R
8081	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Nama Karoo	Karoo National Park	1	M	-11.7	-9.7	4.1						WI	ES	M	R
8082	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Nama Karoo	Karoo National Park	5	-	-10.9	-8.9	3.5	2	13.0	-19.9	-17.9	9.1	WI	ES	M	R
8083	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Nama Karoo	Karoo National Park	1	M	-10.0	-8.0	6.2						WI	ES	M	R
8084	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Nama Karoo	Karoo National Park	1	M	-12.3	-10.3	5.7						WI	ES	M	R
8085	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Nama Karoo	Karoo National Park	5	-	-12.2	-10.2	5.1	2	12.6	-20.0	-18.0	7.9	WI	ES	M	R
8086	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Nama Karoo	Karoo National Park	5	-	-13.5	-11.5	4.1	2	11.8	-20.5	-19.0	7.0	WI	ES	M	R
8087	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Nama Karoo	Karoo National Park	5	-	-11.7	-9.7	5.0						WI	ES	M	R
8088	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Nama Karoo	Karoo National Park	1	M	-10.9	-8.9	4.8						WI	ES	M	R
8089	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Nama Karoo	Karoo National Park	1	M	-9.4	-7.4	4.3						WI	ES	M	R
8090	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Nama Karoo	Karoo National Park	6	-	-11.1	-9.1	3.4	1	11.2	-20.6	-18.6	9.5	WI	ES	M	R
8091	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Nama Karoo	Karoo National Park	1	M	-14.5	-12.5	4.0						WI	ES	M	R
8092	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Nama Karoo	Karoo National Park	1	M	-7.8	-5.8	4.7						WI	ES	M	R

APPENDIX 7

$\delta^{13}C$ and $\delta^{18}O$ results from enamel apatite and $\delta^{13}C$ and $\delta^{15}N$ results from bone collagen for all specimens: An average is reported for duplicate results from one individual

UCT	Type	Feeder Type	Species	Common_name	Biome	Location	N Enamel	Tooth sampled	$\delta^{13}C_{enamel}$	Enamel Fossil fuel adjusted	$\delta^{18}O_{enamel}$	N Collagen	$\delta^{15}N_{collagen}$	$\delta^{13}C_{collagen}$	Collagen Fossil fuel adjusted	$\Delta_{enamel-collagen}$	Water behaviour: WD OR WI	Evaporation sensitivity: ES or EI	Size: S, M, L, or Ex L	R or H fermenter
8093	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Nama Karoo	Karoo National Park	1	M	-11.8	-9.8	5.5						WI	ES	M	R
8094	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Nama Karoo	Karoo National Park	1	M	-11.4	-9.4	4.3						WI	ES	M	R
8095	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Nama Karoo	Karoo National Park	1	M	-12.0	-10.0	6.0						WI	ES	M	R
8096	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Nama Karoo	Karoo National Park	1	M	-8.7	-6.7	2.6						WI	ES	M	R
8097	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Nama Karoo	Karoo National Park	1	M	-11.7	-9.7	5.5						WI	ES	M	R
8098	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Nama Karoo	Karoo National Park	2	-	-13.2	-11.2	6.2	2	12.0	-19.0	-17.0	5.7	WI	ES	M	R
8100	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Nama Karoo	Karoo National Park	1	M	-10.2	-8.2	4.9						WI	ES	M	R
13979	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Nama Karoo	Richmond	1	M^1	-10.6	-8.6	10.1	2	10.0	-19.9	-17.9	9.2	WI	ES	M	R
13993	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Nama Karoo	Richmond	1	M_1	-11.9	-9.9	5.5	2	12.1	-15.6	-13.6	3.7	WI	ES	M	R
14005	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Nama Karoo	Victoria West, Libanon	1	M_1	-13.1	-11.1	3.0	2	9.8	-19.8	-17.8	6.7	WI	ES	M	R
14123	Ungulate	Grazer	*Redunca arundinum*	Southern reedbuck	Nama Karoo	Karoo National Park	1	M^1	-2.2	-0.2	-0.6						WD	EI	M	R
15268	Ungulate	Browser	*Taurotragus oryx*	Eland	Nama Karoo	Augrabies National Park	1	M	-11.7	-9.7	5.5						WI	ES	L	R
15270	Ungulate	Browser	*Diceros bicornis*	Black Rhino	Nama Karoo	Augrabies National Park	1	M	-14.0	-12.0	-1.5	2	6.6	-18.6	-16.6	4.7	WD	EI	Ex L	H
15272	Ungulate	Browser	*Giraffa camelopardalis*	Giraffe	Nama Karoo	Augrabies National Park	1	I	-12.6	-10.6	6.3				2.0		WD	ES	Ex L	R
15274	Ungulate	Browser	*Taurotragus oryx*	Eland	Nama Karoo	Augrabies National Park	1	M	-8.6	-6.6	3.6	2	9.6	-20.2	-18.7	11.6	WI	ES	L	R
15275	Ungulate	Browser	*Tragelaphus strepsiceros*	Kudu	Nama Karoo	Augrabies National Park	1	M	-9.3	-7.3	9.9						WD	ES	L	R
15276	Ungulate	Browser	*Taurotragus oryx*	Eland	Nama Karoo	Augrabies National Park	1	M	-7.8	-5.8	4.5						WI	ES	L	R
15277	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Nama Karoo	Augrabies National Park	1	M	-0.9	1.2	1.9	2	9.0	-8.9	-6.9	8.1	WI	EI	L	R
15278	Ungulate	Browser	*Oreotragus oreotragus*	Klipspringer	Nama Karoo	Augrabies National Park	1	M_1	-11.9	-9.9	2.6	2	10.5	-18.2	-16.2	6.3	WI	ES	S	R
7732	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Savanna	Kgalagadi National Park	1	M^1	-1.5	0.5	5.6	2	11.4	-8.7	-6.7	7.1	WI	EI	L	R
7733	Ungulate	Grazer	*Connochaetes taurinus*	Blue wildebeest	Savanna	Kgalagadi National Park	1	M^2	0.8	2.8	7.7	2	11.4	-9.3	-7.3	10.1	WD	EI	L	R
7734	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Savanna	Kgalagadi National Park	1	M_1	0.0	2.0	2.9	2	11.8	-8.1	-6.1	8.1	WI	EI	L	R
7749	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Savanna	Kgalagadi National Park	2	-	-10.8	-8.8	4.6	2	11.8	-15.3	-13.3	4.5	WI	ES	M	R
7774	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Savanna	Kgalagadi National Park	1	M_1	-1.5	0.5	2.9	2	11.4	-8.5	-6.5	7.0	WI	EI	L	R
7776	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Savanna	Kgalagadi National Park	1	M^1	-2.1	-0.1	10.7	2	11.7	-12.0	-10.0	9.8	WI	EI	L	R
7782	Ungulate	Browser	*Raphicerus campestris*	Steenbok	Savanna	Kgalagadi National Park	1	M^2	-13.6	-11.6	2.7	2	9.3	-19.1	-17.1	5.4	WI	ES	S	R
14013	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Savanna	Kgalagadi National Park	2	-	-3.3	-1.3	7.3	2	11.7	-16.5	-14.5	13.2	WI	EI	L	R
14220	Ungulate	Browser	*Taurotragus oryx*	Eland	Savanna	Kgalagadi National Park	1	M^2	-11.5	-9.5	6.2	2	10.4	-20.7	-18.7	9.2	WI	ES	L	R
14221	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Savanna	Kgalagadi National Park	1	M^2	-1.0	1.0	7.2						WI	EI	L	R
14222	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Savanna	Kgalagadi National Park	1	M^2	-2.4	-0.4	7.8	2	11.2	-12.5	-10.5	10.1	WI	EI	L	R
14223	Ungulate	Browser	*Giraffa camelopardalis*	Giraffe	Savanna	Kgalagadi National Park	1	M^2	-7.3	-5.3	8.5	1	12.4	-20.7	-18.7	13.4	WD	ES	Ex L	R
14224	Ungulate	Grazer	*Connochaetes taurinus*	Blue wildebeest	Savanna	Kgalagadi National Park	1	M^2	-4.6	-2.6	0.8						WD	EI	L	R
14225	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Savanna	Kgalagadi National Park	1	M^1	-2.7	-0.7	6.5	2	10.4	-13.2	-11.2	10.5	WI	EI	L	R
14226	Ungulate	Grazer	*Connochaetes taurinus*	Blue wildebeest	Savanna	Kgalagadi National Park	1	M^2	-0.4	1.6	2.8	2	10.1	-9.1	-7.1	8.8	WD	EI	L	R
14227	Ungulate	Grazer	*Connochaetes taurinus*	Blue wildebeest	Savanna	Kgalagadi National Park	1	M^2	-3.2	-1.2	5.4						WD	EI	L	R
14228	Ungulate	Browser	*Taurotragus oryx*	Eland	Savanna	Kgalagadi National Park	1	M^1	-11.0	-9.0	4.4	2	10.1	-20.3	-18.3	9.3	WI	ES	L	R
14229	Ungulate	Grazer	*Connochaetes taurinus*	Blue wildebeest	Savanna	Kgalagadi National Park	1	M^2	-3.5	-1.5	1.7						WD	EI	L	R
14230	Ungulate	Browser	*Taurotragus oryx*	Eland	Savanna	Kgalagadi National Park	1	M^2	-11.6	-9.6	5.1	2	9.5	-20.8	-18.8	9.2	WI	ES	L	R
14231	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Savanna	Kgalagadi National Park	1	M^2	-3.1	-1.1	6.2	2	10.8	-12.2	-10.2	9.0	WI	EI	L	R
14232	Ungulate	Grazer	*Connochaetes taurinus*	Blue wildebeest	Savanna	Kgalagadi National Park	1	M^1	-2.5	-0.5	2.6						WD	EI	L	R
14233	Ungulate	Grazer	*Connochaetes taurinus*	Blue wildebeest	Savanna	Kgalagadi National Park	1	M^2	-1.9	0.1	3.1	2	9.5	-10.2	-8.2	8.3	WD	EI	L	R
14234	Ungulate	Grazer	*Connochaetes taurinus*	Blue wildebeest	Savanna	Kgalagadi National Park	1	M^1	0.6	2.6	-0.5	2	9.3	-8.9	-6.9	9.5	WD	EI	L	R
14235	Ungulate	Browser	*Taurotragus oryx*	Eland	Savanna	Kgalagadi National Park	1	M^1	-10.9	-8.9	6.7						WI	ES	L	R
14236	Ungulate	Browser	*Taurotragus oryx*	Eland	Savanna	Kgalagadi National Park	1	M^2	-10.7	-8.7	9.0	2	12.6	-20.7	-18.7	10.0	WI	ES	L	R
14237	Ungulate	Browser	*Taurotragus oryx*	Eland	Savanna	Kgalagadi National Park	1	M^2	-11.1	-9.1	7.6						WI	ES	L	R
14238	Ungulate	Browser	*Taurotragus oryx*	Eland	Savanna	Kgalagadi National Park	1	M^2	-15.6	-13.6	2.8						WI	ES	L	R
14239	Ungulate	Browser	*Taurotragus oryx*	Eland	Savanna	Kgalagadi National Park	1	M^2	-13.1	-11.1	5.3						WI	ES	L	R
14240	Ungulate	Browser	*Taurotragus oryx*	Eland	Savanna	Kgalagadi National Park	1	M^1	-15.6	-13.6	6.9	2	9.3	-19.6	-17.6	4.0	WI	ES	L	R
14241	Ungulate	Browser	*Taurotragus oryx*	Eland	Savanna	Kgalagadi National Park	1	M^1	-13.5	-11.5	9.1	2	9.7	-20.6	-18.6	7.1	WI	ES	L	R

APPENDIX 7

$\delta^{13}C$ and $\delta^{18}O$ results from enamel apatite and $\delta^{13}C$ and $\delta^{15}N$ results from bone collagen for all specimens: An average is reported for duplicate results from one individual

UCT	Type	Feeder Type	Species	Common_name	Biome	Location	N Enamel	Tooth sampled	$\delta^{13}C_{enamel}$	Enamel Fossil fuel adjusted	$\delta^{18}O_{enamel}$	N Collagen	$\delta^{15}N_{collagen}$	$\delta^{13}C_{collagen}$	Collagen Fossil fuel adjusted	$\Delta_{enamel-collagen}$	Water behaviour: WD OR WI	Evaporation sensitivity: ES or EI	Size: S, M, L, or Ex L	R or H fermenter
14242	Ungulate	Browser	*Taurotragus oryx*	Eland	Savanna	Kgalagadi National Park	1	M^1	-12.6	-10.6	4.9	2	9.8	-19.8	-17.8	7.2	WI	ES	L	R
14243	Ungulate	Browser	*Taurotragus oryx*	Eland	Savanna	Kgalagadi National Park	1	M^1	-12.9	-10.9	6.1	3	9.9	-19.0	-17.0	6.1	WI	ES	L	R
14244	Ungulate	Browser	*Taurotragus oryx*	Eland	Savanna	Kgalagadi National Park	1	M^1	-13.3	-11.3	8.5	2	10.5	-19.8	-17.8	6.5	WI	ES	L	R
14245	Ungulate	Browser	*Taurotragus oryx*	Eland	Savanna	Kgalagadi National Park	1	M_1	-15.3	-13.3	2.1	2	10.0	-19.8	-17.8	4.6	WI	ES	L	R
14246	Ungulate	Browser	*Taurotragus oryx*	Eland	Savanna	Kgalagadi National Park	1	M^1	-9.9	-7.9	6.8	2	10.5	-21.0	-19.0	11.1	WI	ES	L	R
14247	Ungulate	Browser	*Taurotragus oryx*	Eland	Savanna	Kgalagadi National Park	1	M^1	-11.4	-9.4	8.5	2	11.4	-20.0	-18.0	8.6	WI	ES	L	R
14248	Ungulate	Browser	*Taurotragus oryx*	Eland	Savanna	Kgalagadi National Park	1	M^1	-15.3	-13.3	3.2	2	10.3	-20.0	-18.0	4.7	WI	ES	L	R
14249	Ungulate	Browser	*Taurotragus oryx*	Eland	Savanna	Kgalagadi National Park	1	M^1	-16.3	-14.3	2.2	2	10.6	-19.9	-17.9	3.6	WI	ES	L	R
14250	Ungulate	Browser	*Taurotragus oryx*	Eland	Savanna	Kgalagadi National Park	1	M^1	-8.1	-6.1	9.0	2	12.0	-19.2	-17.2	11.1	WI	ES	L	R
14251	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Savanna	Kgalagadi National Park	1	M^1	-10.7	-8.7	3.3	2	10.6	-16.9	-14.9	6.2	WI	ES	M	R
14252	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Savanna	Kgalagadi National Park	1	M^1	-10.1	-8.1	5.2	2	10.2	-17.6	-15.6	7.5	WI	ES	M	R
14253	Ungulate	Grazer	*Connochaetes taurinus*	Blue wildebeest	Savanna	Kgalagadi National Park	1	M^2	-2.0	0.0	1.9						WD	EI	L	R
14254	Ungulate	Grazer	*Connochaetes taurinus*	Blue wildebeest	Savanna	Kgalagadi National Park	1	M^2	-3.8	-1.8	4.0						WD	EI	L	R
14255	Ungulate	Grazer	*Connochaetes taurinus*	Blue wildebeest	Savanna	Kgalagadi National Park	1	M^2	1.6	3.6	-1.7	1	10.9	-8.6	-6.6	10.3	WD	EI	L	R
14256	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Savanna	Kgalagadi National Park	1	M^2	-4.5	-2.5	4.2	2	9.2	-14.2	-12.2	9.7	WI	EI	L	R
14257	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Savanna	Kgalagadi National Park	1	M^1	-5.9	-3.9	8.3	2	10.1	-12.1	-10.1	6.2	WI	EI	L	R
14258	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Savanna	Kgalagadi National Park	1	M^1	-4.3	-2.3	4.0	2	9.2	-12.2	-10.2	7.9	WI	EI	L	R
14259	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Savanna	Kgalagadi National Park	1	M^1	-1.5	0.5	6.7	2	9.9	-11.6	-9.6	10.1	WI	EI	L	R
14260	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Savanna	Kgalagadi National Park	1	M^1	-5.7	-3.7	3.1						WI	EI	L	R
14261	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Savanna	Kgalagadi National Park	1	M^2	-1.6	0.4	8.5						WI	EI	L	R
14262	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Savanna	Kgalagadi National Park	1	M^2	-0.6	1.4	6.5	2	9.7	-9.1	-7.1	8.5	WI	EI	L	R
14263	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Savanna	Kgalagadi National Park	1	P^4	-0.5	1.5	6.6	2	12.3	-9.8	-7.8	9.3	WI	EI	L	R
14264	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Savanna	Kgalagadi National Park	1	M^1	0.4	2.4	6.1	2	10.3	-9.3	-7.3	9.7	WI	EI	L	R
14265	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Savanna	Kgalagadi National Park	1	M^1	-4.3	-2.3	2.6	2	9.0	-13.0	-11.0	8.7	WI	EI	L	R
14266	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Savanna	Kgalagadi National Park	1	M^1	-11.9	-9.9	4.3	2	9.3	-17.8	-15.8	5.9	WI	ES	M	R
14267	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Savanna	Kgalagadi National Park	1	M^1	-3.1	-1.1	8.1	2	10.6	-12.8	-10.8	9.7	WI	EI	L	R
14268	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Savanna	Kgalagadi National Park	1	M_1	-7.1	-5.1	5.2	2	8.9	-13.1	-11.1	6.0	WI	EI	L	R
14272	Ungulate	Grazer	*Damaliscus pygargus pyga*	Bontebok	Savanna	Kgalagadi National Park	1	M^1	-4.7	-2.7	-0.7	2	8.2	-14.9	-12.9	10.2	WD	EI	M	R
4290	Ungulate	Browser	*Raphicerus campestris*	Steenbok	Succulent Karoo	Botterkloof, Doornbos	3	-	-10.3	-8.3	5.4	2	14.1	-14.8	-12.8	4.5	WI	ES	S	R
8101	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Succulent Karoo	Anysberg	2	-	-10.4	-8.4	4.9						WI	ES	M	R
8102	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Succulent Karoo	Anysberg	1	M	-9.9	-7.9	6.1						WI	ES	M	R
8103	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Succulent Karoo	Anysberg	1	M	-11.9	-9.9	5.2						WI	ES	M	R
8104	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Succulent Karoo	Anysberg	5	-	-13.3	-11.3	5.3	2	11.5	-19.4	-17.4	6.1	WI	ES	M	R
8105	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Succulent Karoo	Anysberg	1	M	-10.7	-8.7	5.6						WI	ES	M	R
8106	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Succulent Karoo	Anysberg	1	M	-12.1	-10.1	5.4	2	12.2	-20.7	-18.7	8.6	WI	ES	M	R
8113	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Succulent Karoo	Anysberg	1	M	-11.9	-9.9	5.0						WI	ES	M	R
13980	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Succulent Karoo	Anysberg	1	M_1	-12.9	-10.9	1.9	2	7.7	-19.8	-17.8	6.9	WI	ES	S	R
13981	Ungulate	Browser	*Pelea capreolus*	Grey rhebuck	Succulent Karoo	Anysberg	1	M_1	-13.3	-11.3	3.8	2	11.3	-19.1	-17.1	5.8	WI	ES	S	R
13982	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Succulent Karoo	Anysberg	1	M_1	-12.8	-10.8	6.6	2	7.8	-20.1	-18.1	7.3	WI	ES	S	R
13983	Ungulate	Browser	*Oreotragus oreotragus*	Klipspringer	Succulent Karoo	Anysberg	1	M^1	-13.0	-11.0	4.1	2	7.7	-20.2	-18.2	7.2	WI	ES	S	R
13984	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Succulent Karoo	Anysberg	1	M^1	-13.3	-11.3	2.4	2	4.6	-19.9	-17.9	6.6	WI	ES	S	R
13985	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Succulent Karoo	Anysberg	1	M_1	-11.7	-9.7	3.8	2	10.5	-18.5	-16.5	6.8	WI	ES	S	R
13986	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Succulent Karoo	Anysberg	1	M_1	-13.7	-11.7	3.8	4	7.9	-20.1	-18.1	6.5	WI	ES	S	R
13990	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Succulent Karoo	Anysberg	1	M^1	-10.8	-8.8	4.1	2	10.6	-18.5	-16.5	7.7	WI	ES	M	R
13999	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Succulent Karoo	Anysberg	1	M_1	-14.2	-12.2	1.6	2	10.6	-16.7	-14.7	2.5	WI	EI	L	R
14000	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Succulent Karoo	Anysberg	1	M^1	-2.7	-0.7	0.7	3	11.1	-11.3	-9.3	8.6	WI	EI	L	R
14001	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Succulent Karoo	Anysberg	1	M_1	-1.3	0.7	1.5	3	12.0	-11.7	-9.7	10.5	WI	EI	L	R
14002	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Succulent Karoo	Anysberg	1	M_1	-7.6	-5.6	2.5	2	12.4	-12.2	-10.2	4.7	WI	EI	L	R
14003	Ungulate	Browser	*Taurotragus oryx*	Eland	Succulent Karoo	Anysberg	1	M^1	-13.2	-11.2	-1.3	2	4.5	-23.2	-21.2	10.0	WI	ES	L	R

APPENDIX 7

$\delta^{13}C$ and $\delta^{18}O$ results from enamel apatite and $\delta^{13}C$ and $\delta^{15}N$ results from bone collagen for all specimens: An average is reported for duplicate results from one individual

UCT	Type	Feeder Type	Species	Common_name	Biome	Location	N Enamel	Tooth sampled	$\delta^{13}C_{enamel}$	Enamel Fossil fuel adjusted	$\delta^{18}O_{enamel}$	N Collagen	$\delta^{15}N_{collagen}$	$\delta^{13}C_{collagen}$	Collagen Fossil fuel adjusted	$\Delta_{enamel\text{-}collagen}$	Water behaviour: WD OR WI	Evaporation sensitivity: ES or EI	Size: S, M, L, or Ex L	R or H fermenter
14019	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Succulent Karoo	Hester Malan Nature rese	1	M_1	-7.0	-5.0	1.4						WI	ES	M	R
14035	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Succulent Karoo	Anysberg	1	M_1	-3.3	-1.3	2.3						WI	EI	L	R
14036	Ungulate	Browser	*Tragelaphus strepsiceros*	Kudu	Succulent Karoo	Anysberg	1	M^1	-14.7	-12.7	4.5						WD	ES	L	R
14037	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Succulent Karoo	Anysberg	1	M_1	-12.0	-10.0	-0.5						WI	ES	M	R
14038	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Succulent Karoo	Anysberg	1	M_1	-16.6	-14.6	3.6						WI	ES	M	R
14039	Ungulate	Grazer	*Equus burchelli*	Burchell's Zebra	Succulent Karoo	Anysberg	1	P_2	-4.1	-2.1	-0.6						WD	EI	L	H
14040	Ungulate	Browser	*Oreotragus oreotragus*	Klipspringer	Succulent Karoo	Anysberg	1	M_1	-13.1	-11.1	1.3						WI	ES	S	R
14041	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Succulent Karoo	Anysberg	1	M^1	-2.4	-0.4	0.0						WI	EI	L	R
14047	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Succulent Karoo	Anysberg	1	M_1	-14.4	-12.4	3.1						WI	ES	S	R
14306	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Succulent Karoo	Namaqua National Park	1	M_1	-1.0	1.0	2.7						WI	EI	L	R
14307	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Succulent Karoo	Namaqua National Park	1	M_1	-2.3	-0.3	-0.2	2	15.4	-18.4	-16.4	16.1	WI	EI	L	R
14308	Ungulate	Grazer	*Alcelaphus buselaphus*	Red hartebeest	Succulent Karoo	Namaqua National Park	1	M_1	-5.0	-3.0	3.9	2	12.4	-11.8	-9.8	6.7	WI	EI	L	R
15269	Ungulate	Browser	*Raphicerus campestris*	Steenbok	Succulent Karoo	Knersvlakte	1	M_1	-11.5	-9.5	-1.5	2	17.2	-15.0	-13.0	3.6	WI	ES	S	R
15273	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Succulent Karoo	Namaqua National Park	1	M_2	-13.4	-11.4	1.8	2	11.1	-21.3	-19.3	7.9	WI	ES	M	R
15404	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Succulent Karoo	Anysberg	1	M^1	-13.9	-11.9	1.8	2	12.1	-19.4	-17.4	5.5	WI	ES	S	R
15405	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Succulent Karoo	Anysberg	1	M^1	-13.6	-11.6	1.6	2	11.5	-18.8	-16.8	5.2	WI	ES	S	R
15406	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Succulent Karoo	Anysberg	1	M_1	-15.7	-13.7	-3.0	2	10.8	-19.7	-17.7	4.0	WI	ES	S	R
15407	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Succulent Karoo	Anysberg	1	M^1	-12.2	-10.2	-2.7	2	11.8	-18.2	-16.2	6.0	WI	ES	S	R
15408	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Succulent Karoo	Anysberg	1	M^1	-14.2	-12.2	5.5	2	10.9	-19.7	-17.7	5.5	WI	ES	S	R
15409	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Succulent Karoo	Anysberg	1	M^1	-14.5	-12.5	4.7	4	10.6	-20.5	-18.5	6.0	WI	ES	S	R
15410	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Succulent Karoo	Anysberg	1	M_1	-14.3	-12.3	3.4	2	11.6	-18.5	-16.5	4.3	WI	ES	S	R
15411	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Succulent Karoo	Anysberg	1	M_1	-14.5	-12.5	3.8	2	11.9	-18.6	-16.6	4.1	WI	ES	S	R
15412	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Succulent Karoo	Anysberg	1	M_1	-14.2	-12.2	3.8	2	10.2	-20.1	-18.1	5.9	WI	ES	S	R
15413	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Succulent Karoo	Anysberg	1	M^1	-10.5	-8.5	4.3	2	7.7	-18.8	-16.8	8.4	WI	ES	S	R
15414	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Succulent Karoo	Anysberg	1	M^1	-14.5	-12.5	4.4	2	9.8	-20.7	-18.7	6.2	WI	ES	S	R
15415	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Succulent Karoo	Anysberg	1	M_1	-13.2	-11.2	-4.2	2	12.5	-17.6	-15.6	4.4	WI	ES	S	R
15416	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Succulent Karoo	Anysberg	1	M_1	-13.1	-11.1	-8.1	2	11.2	-18.9	-16.9	5.8	WI	ES	S	R
15417	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Succulent Karoo	Anysberg	1	M_1	-14.7	-12.7	0.3	2	6.5	-20.0	-18.0	5.3	WI	ES	S	R
15418	Ungulate	Browser	*Sylvicapra grimmia*	Common duiker	Succulent Karoo	Anysberg	1	M_1	-11.1	-9.1	1.8	3	12.7	-19.4	-17.4	8.3	WI	ES	S	R
15419	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Succulent Karoo	Anysberg	1	M_1	-12.5	-10.5	5.5	2	12.4	-19.3	-17.3	6.8	WI	ES	M	R
15420	Ungulate	Mixed	*Antidorcas marsupialis*	Springbok	Succulent Karoo	Anysberg	1	M_1	-10.9	-8.9	2.0	2	10.3	-18.1	-16.1	7.2	WI	ES	M	R
15421	Ungulate	Grazer	*Equus zebra*	Mountain zebra	Succulent Karoo	Anysberg	1	M_1	-5.2	-3.2	3.1	2	9.4	-14.9	-12.9	9.8	WD	EI	L	H
15422	Ungulate	Grazer	*Equus zebra*	Mountain zebra	Succulent Karoo	Anysberg	1	M_1	-5.8	-3.8	-0.3	2	9.7	-14.5	-12.5	8.7	WD	EI	L	H
15423	Ungulate	Browser	*Raphicerus sp*	Steenbok/Grysbok	Succulent Karoo	Anysberg	1	M_1	-14.1	-12.1	-2.4	2	4.3	-20.1	-18.1	6.0	WI	ES	S	R
15424	Ungulate	Browser	*Raphicerus sp*	Steenbok/Grysbok	Succulent Karoo	Anysberg	1	M_1	-14.0	-12.0	2.6	2	13.3	-19.3	-17.3	5.3	WI	ES	S	R
15425	Ungulate	Browser	*Raphicerus sp*	Steenbok/Grysbok	Succulent Karoo	Anysberg	1	M_1	-12.6	-10.6	1.5	2	12.4	-17.9	-15.9	5.3	WI	ES	S	R
15426	Ungulate	Browser	*Raphicerus sp*	Steenbok/Grysbok	Succulent Karoo	Anysberg	1	M_1	-13.6	-11.6	0.5	2	4.0	-20.7	-18.7	7.1	WI	ES	S	R
15427	Ungulate	Browser	*Raphicerus sp*	Steenbok/Grysbok	Succulent Karoo	Anysberg	1	M_1	-14.1	-12.1	3.3	2	4.1	-19.9	-17.9	5.8	WI	ES	S	R
15428	Ungulate	Browser	*Raphicerus sp*	Steenbok/Grysbok	Succulent Karoo	Anysberg	1	M_1	-14.4	-12.4	-1.6	2	12.4	-19.8	-17.8	5.4	WI	ES	S	R
15429	Ungulate	Browser	*Raphicerus sp*	Steenbok/Grysbok	Succulent Karoo	Anysberg	1	M_1	-14.8	-12.8	2.5	2	13.0	-19.3	-17.3	4.6	WI	ES	S	R
16213	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Succulent Karoo	Anysberg	1	M_1	-1.2	0.8	2.3	2	9.8	-11.5	-9.5	10.3	WI	EI	L	R
16214	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Succulent Karoo	Anysberg	1	M_1	-3.4	-1.4	0.0	2	10.5	-13.9	-11.9	10.5	WI	EI	L	R
16215	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Succulent Karoo	Anysberg	1	M_1	-12.0	-10.0	-0.7	2	8.5	-19.4	-17.4	7.4	WI	EI	L	R
16216	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Succulent Karoo	Anysberg	1	M_1	-3.2	-1.2	1.7	2	10.5	-9.9	-7.9	6.6	WI	EI	L	R
16217	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Succulent Karoo	Anysberg	1	M_1	-11.5	-9.5	0.2	2	8.4	-18.9	-16.9	7.4	WI	EI	L	R
16218	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Succulent Karoo	Anysberg	1	M_1	-2.1	-0.1	0.7	2	10.3	-16.0	-14.0	13.9	WI	EI	L	R
16219	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Succulent Karoo	Anysberg	1	M_1	-8.2	-6.2	2.6	2	11.7	-17.4	-15.4	9.1	WI	EI	L	R
16220	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Succulent Karoo	Anysberg	1	M_1	-2.7	-0.7	2.5	2	10.2	-9.7	-7.7	7.0	WI	EI	L	R
16385	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Succulent Karoo	Anysberg	3	-	-7.5	-5.5	2.9	2	10.9	-16.8	-14.8	9.3	WI	EI	L	R

APPENDIX 7

$\delta^{13}C$ and $\delta^{18}O$ results from enamel apatite and $\delta^{13}C$ and $\delta^{15}N$ results from bone collagen for all specimens: An average is reported for duplicate results from one individual

UCT	Type	Feeder Type	Species	Common_name	Biome	Location	N Enamel	Tooth sampled	$\delta^{13}C_{enamel}$	Enamel Fossil fuel adjusted	$\delta^{18}O_{enamel}$	N Collagen	$\delta^{15}N_{collagen}$	$\delta^{13}C_{collagen}$	Collagen Fossil fuel adjusted	$\Delta_{enamel-collagen}$	Water behaviour: WD OR WI	Evaporation sensitivity: ES or EI	Size: S, M, L, or Ex L	R or H fermenter
16386	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Succulent Karoo	Anysberg	2	-	-10.0	-8.0	3.2	2	11.3	-14.5	-12.5	4.5	WI	EI	L	R
16387	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Succulent Karoo	Anysberg	3	-	-4.2	-2.2	4.3	2	10.5	-15.8	-13.8	11.6	WI	EI	L	R
16388	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Succulent Karoo	Anysberg	3	-	-8.1	-6.1	3.7	2	9.1	-18.4	-16.4	10.2	WI	EI	L	R
16389	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Succulent Karoo	Anysberg	3	-	-5.2	-3.2	2.3	2	10.5	-17.2	-15.2	12.1	WI	EI	L	R
16390	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Succulent Karoo	Anysberg	2	-	-12.0	-10.0	1.6	2	10.0	-14.1	-12.1	2.1	WI	EI	L	R
16391	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Succulent Karoo	Anysberg	2	-	-12.4	-10.4	2.2	2	10.7	-16.5	-14.5	4.1	WI	EI	L	R
16392	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Succulent Karoo	Anysberg	3	-	-7.9	-5.9	3.5	2	10.5	-16.4	-14.4	8.5	WI	EI	L	R
16393	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Succulent Karoo	Anysberg	3	-	-5.5	-3.5	2.9	2	11.1	-17.0	-15.0	11.5	WI	EI	L	R
16394	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Succulent Karoo	Anysberg	2	-	-13.4	-11.4	1.8	2	11.0	-15.3	-13.3	1.9	WI	EI	L	R
16395	Ungulate	Grazer	*Oryx gazella*	Gemsbok	Succulent Karoo	Anysberg	2	-	-12.1	-10.1	1.4	2	11.5	-16.4	-14.4	4.3	WI	EI	L	R

Note: Where no number or position is indicated, then it is unknown (mostly due to samples being isolated teeth)

APPENDIX 8

Appendix 8a: Summary statistics for $\delta^{13}C_{enamel}$ for each group discussed in Results

OVERALL

Type	Feeder Type	N	Median	Minimum	Maximum	Mean	Std. Deviation
Carnivore	Carnivore	33	-12.6	-18.2	-4.9	-12.1	3.1
Primate	Omnivore	146	-14.5	-17.1	-5.2	-14	2.3
Ungulate		297	-10.9	-18.9	2	-9.1	5.3
	Browser	121	-13.5	-18.9	-7.3	-13.2	2.3
	Grazer	121	-3.2	-14.2	2	-3.7	3.4
	Mixed feeder	41	-11.7	-16.6	-7	-11.4	1.7
	Omnivore	14	-14.8	-17.5	-8.9	-14.6	1.9

$\delta^{13}C_{enamel}$ for all animal groups highlighting differences across biomes

BY FEEDER TYPE

Biome	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany Thicket	22	-12.0	-18.1	-8.1	-12.1	2.7
Forest	11	-15.4	-18.5	-13.4	-15.9	1.7
Fynbos	26	-14.2	-18.9	-8.8	-13.8	2.2
Nama Karoo	7	-10.8	-14.0	-7.8	-10.8	2.3
Savanna	21	-12.6	-16.3	-7.3	-12.4	2.4
Succulent Karoo	34	-13.6	-15.7	-10.5	-13.5	1.1

$\delta^{13}C_{enamel}$ of browsing ungulate species highlighting differences across biomes

Biome	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany Thicket	52	-3.0	-10.7	2	-2.7	2.7
Fynbos	3	-7.7	-10	-5.1	-7.6	2.4
Nama Karoo	2	-1.5	-2.2	-0.9	-1.5	0.9
Savanna	33	-2.4	-7.1	1.6	-2.4	2.1
Succulent Karoo	31	-5.2	-14.2	-1	-6.4	4.1

$\delta^{13}C_{enamel}$ of grazing ungulate species highlighting differences across biomes

Biome	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany Thicket						
Forest						
Fynbos						
Nama Karoo	23	-11.7	-14.5	-7.8	-11.4	1.5
Savanna	4	-10.8	-11.9	-10.1	-10.9	0.7
Succulent Karoo	14	-11.9	-16.6	-7	-11.7	2.1

$\delta^{13}C_{enamel}$ of mixed feeding ungulate species highlighting differences across biomes

	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany thicket	0					
Forest	13	-15.1	-17.5	-14	-15.1	1
Fynbos	1	-8.9	-8.9	-8.9	-8.9	
Nama Karoo	0					
Savanna	0					
Succulent Karoo	0					

$\delta^{13}C_{enamel}$ of omnivorous ungulate species highlighting differences across biomes

Appendix 8a: Summary statistics for $\delta^{13}C_{enamel}$ for each group discussed in Results

	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany thicket	2	-8.8	-9.9	-7.8	-8.9	1.4
Forest	7	-13.6	-18.2	-9.7	-13.6	2.5
Fynbos	14	-14.4	-16.6	-9.8	-14	1.8
Nama Karoo	1	-11.4	-11.4	-11.4	-11.4	
Savanna	8	-8.9	-10.6	-4.9	-8.5	1.8
Succulent Karoo	1	-8.8	-8.8	-8.8	-8.8	

$\delta^{13}C_{enamel}$ of carnivores highlighting differences across biomes

Biome	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany Thicket	8	-6.7	-7.6	-5.2	-6.6	0.8
Forest	11	-15.5	-17	-14	-15.6	0.9
Fynbos	98	-14.8	-17.1	-8.8	-14.6	1.4
Nama Karoo						
Savanna						
Succulent Karoo	29	-13.7	-15.1	-5.2	-13.5	1.7

$\delta^{13}C_{enamel}$ of primates highlighting differences across biomes

By BIOME

FeederType	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	22	-12.0	-18.1	-8.1	-12.1	2.7
Carnivore	2	-8.8	-9.9	-7.8	-8.8	1.4
Grazer	52	-3.0	-10.7	2	-2.7	2.7
Omnivore	8	-6.7	-7.6	-5.2	-6.6	0.8

$\delta^{13}C_{enamel}$ of all species from the Albany Thicket biome

	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	11	-15.4	-18.5	-13.4	-15.9	1.7
Grazer	0					
Omnivore	24	-15.2	-17.5	-14	-15.3	1
Carnivore	7	-13.6	-18.2	-9.7	-13.6	2.5

$\delta^{13}C_{enamel}$ of all species from the Forest biome

FeederType	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	26	-14.2	-18.9	-8.8	-13.8	2.2
Carnivore	14	-14.4	-16.6	-9.8	-14	1.8
Grazer	3	-7.7	-10	-5.1	-7.6	2.4
Omnivore	99	-14.8	-17.1	-8.8	-14.5	1.5

$\delta^{13}C_{enamel}$ of all species from the Fynbos biome

FeederType	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	7	-10.8	-14	-7.8	-10.8	2.3
Carnivore	1	-11.4	-11.4	-11.4	-11.4	
Grazer	2	-1.5	-2.2	-0.9	-1.5	0.9
Mixed	23	-11.7	-14.5	-7.8	-11.4	1.5

$\delta^{13}C_{enamel}$ of all species from the Nama Karoo biome

Appendix 8a: Summary statistics for $\delta^{13}C_{enamel}$ for each group discussed in Results

	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	21	-12.6	-16.3	-7.3	-12.4	2.4
Carnivore	8	-8.9	-10.5	-4.9	-8.5	1.8
Grazer	33	-2.4	-7.1	1.6	-2.4	2.1
Mixed	4	-10.8	-11.9	-10.1	-10.9	0.7
Omnivore						

$\delta^{13}C_{enamel}$ of all species from the Savanna biome

FeederType	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	34	-13.6	-15.7	-10.5	-13.5	1.1
Carnivore	1	-8.8	-8.8	-8.8	-8.8	
Grazer	31	-5.2	-14.2	-1	-6.4	4.1
Mixed	14	-11.9	-16.6	-7	-11.7	2.1
Omnivore	29	-13.7	-15.1	-5.2	-13.5	1.7

$\delta^{13}C_{enamel}$ of all species from the Succulent Karoo biome

Appendix 8b: Summary statistics for $\delta^{18}O_{enamel}$ for each group discussed in Results

OVERALL

Type	Feeder Type	N	Median	Minimum	Maximum	Mean	Std. Deviation
Carnivore	Carnivore	33	-2.5	-10	2.2	-3.0	3.1
Primate	Omnivore	146	-0.7	-9.3	2.7	-1.0	2.5
Ungulate		297	1.8	-11.3	10.7	1.5	4.1
Browser	Browser	121	1.8	-9.2	9.9	1.6	4.2
Grazer	Grazer	121	1.1	-10.8	10.7	1.2	3.6
Mixed	Mixed feeder	41	4.8	-0.5	10.1	4.5	1.7
Omnivore	Omnivore	14	-5.3	-11.3	-3.1	-5.9	2.1

$\delta^{18}O$ of all animal groups highlighting differences across biomes

BY Feeding preference

Biome	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany Thicket	22	1.2	-5.5	3.6	0.4	2.1
Forest	11	-5.9	-9.2	-3.9	-6.8	1.9
Fynbos	26	1.0	-3	8.8	1.7	3
Nama Karoo	7	5.0	-1.5	9.9	4.4	3.5
Savanna	21	6.2	2.1	9.1	6	2.4
Succulent Karoo	34	2.5	-8.1	6.6	1.7	3.2

$\delta^{18}O$ of browsing ungulate species highlighting differences across biomes

Biome	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany Thicket	52	-0.1	-10.8	3.4	-1.2	3
Forest						
Fynbos	3	-2.6	-5.2	-1.7	-3.2	1.8
Nama Karoo	2	0.6	-0.6	1.9	0.6	1.8
Savanna	33	5.2	-1.7	10.7	4.7	3
Succulent Karoo	31	2.2	-0.7	4.3	1.8	1.4

$\delta^{18}O$ of grazing ungulate species highlighting differences across biomes

Biome	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany Thicket						
Forest						
Fynbos						
Nama Karoo	23	4.8	2.6	10.1	4.9	1.5
Savanna	4	4.4	3.3	5.2	4.3	0.8
Succulent Karoo	14	4.9	-0.5	6.1	4	2

$\delta^{18}O$ of mixed feeding ungulate species highlighting differences across biomes

	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany thicket						
Forest	13	-5.5	-11.3	-3.9	-6.1	1.9
Fynbos	1	-3.1	-3.1	-3.1	-3.1	
Nama Karoo						
Savanna						
Succulent Karoo						

$\delta^{18}O$ of omnivorous ungulates highlighting differences across biomes

Appendix 8b: Summary statistics for $\delta^{18}O_{enamel}$ for each group discussed in Results

	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany thicket	2	-1.0	-2.5	0.4	-1	2.1
Forest	7	-8.8	-10	-2.8	-7.2	2.8
Fynbos	14	-2.2	-3.7	0.9	-1.9	1.4
Nama Karoo	1	-4.8	-4.8	-4.8	-4.8	
Savanna	8	-2.7	-6.6	2.2	-2.3	2.7
Succulent Karoo	1	2.0	2	2	2	

$\delta^{18}O$ of carnivores highlighting differences across biomes

	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany thicket	8	1.4	-2.6	2.7	0.5	2.1
Forest	11	-3.9	-6.2	-1.2	-3.2	1.6
Fynbos	98	-0.9	-9.3	2.7	-1.4	2.4
Nama Karoo						
Savanna						
Succulent Karoo	29	1.3	-4.7	2.5	0.8	1.7

$\delta^{18}O$ of primates highlighting differences across biomes

BY BIOME

FeederType	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	22	1.2	-5.5	3.6	0.4	2.1
Carnivore	2	-1.0	-2.5	0.4	-1	2.1
Grazer	52	-0.1	-10.8	3.4	-1.2	3
Omnivore	8	1.4	-2.6	2.7	0.5	2.1

$\delta^{18}O$ of all species from the Albany Thicket biome

	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	11	-5.9	-9.2	-3.9	-6.8	1.9
Carnivore	7	-8.8	-10	-2.8	-7.2	2.8
Grazer						
Omnivore	24	-4.9	-11.3	-1.2	-4.8	2.3

$\delta^{18}O$ of all species from the Forest biome

FeederType	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	26	1.0	-3	8.8	1.7	3
Carnivore	14	-2.2	-3.7	0.9	-1.9	1.4
Grazer	3	-2.6	-5.2	-1.7	-3.2	1.8
Omnivore	99	-0.9	-9.3	2.7	-1.4	2.4

$\delta^{18}O$ of all species from the Fynbos biome

FeederType	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	7	5.0	-1.5	9.9	4.4	3.5
Carnivore	1	-4.8	-4.8	-4.8	-4.8	
Grazer	2	0.6	-0.6	1.9	0.6	1.8
Mixed	23	4.8	2.6	10.1	4.9	1.5

$\delta^{18}O$ of all species from the Nama Karoo biome

Appendix 8b: Summary statistics for $\delta^{18}O_{enamel}$ for each group discussed in Results

	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	21	6.2	2.1	9.1	6	2.4
Carnivore	8	-2.7	-6.6	2.2	-2.3	2.7
Grazer	33	5.2	-1.7	10.7	4.7	3
Mixed	4	4.4	3.3	5.2	4.3	0.8
Omnivore						

$\delta^{18}O$ of all species from the Savanna biome

FeederType	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	34	2.5	-8.1	6.6	1.7	3.2
Carnivore	1	2.0	2	2	2	
Grazer	31	2.2	-0.7	4.3	1.8	1.4
Mixed	14	4.9	-0.5	6.1	4	2
Omnivore	29	1.3	-4.7	2.5	0.8	1.7

$\delta^{18}O$ of all species from the Succulent Karoo biome

BY ES/EI

Biome	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany Thicket	34	-0.4	-10.8	3.6	-1.6	3.3
Forest	6	-5.9	-8.6	-4.6	-6.4	1.5
Fynbos	25	0.9	-3	8.5	1.2	2.6
Nama Karoo	29	4.7	1.9	10.1	4.8	1.7
Savanna	45	6.1	2.1	10.7	5.8	2.2
Succulent Karoo	76	2.4	-8.1	6.6	2.2	2.6

$\delta^{18}O$ of Water Independent ungulate species from all biomes

Biome	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany Thicket	40	0.5	-6.3	3.4	0.1	2.1
Forest	18	-5.6	-11.3	-1.2	-6.4	2.1
Fynbos	3	-3.1	-5.2	-2.6	-3.6	1.4
Nama Karoo	4	2.9	-1.5	9.9	3.5	5.5
Savanna	13	2.6	-1.7	8.5	2.7	3.1
Succulent Karoo	4	1.4	-0.6	4.5	1.7	2.5

$\delta^{18}O$ of Water Dependent ungulate species from all biomes

Biome	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany Thicket	22	1.2	-5.5	3.6	0.4	2.1
Forest	10	-6.8	-9.2	-4.6	-7	2.1
Fynbos	24	1.0	-3	8.5	1.3	3.1
Nama Karoo	30	4.9	2.6	10.1	5.1	2.5
Savanna	25	5.3	2.1	9.1	5.7	4.2
Succulent Karoo	49	3.3	-8.1	6.6	2.4	3

$\delta^{18}O$ of Evaporation Sensitive ungulate species from all biomes

Biome	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany Thicket	52	-0.1	-10.8	3.4	-1.2	3
Forest	14	-5.3	-11.3	-3.9	-5.9	2
Fynbos	4	-2.8	-5.2	-1.7	-3.1	1.5
Nama Karoo	4	-0.6	-1.5	1.9	-0.1	1.8
Savanna	33	5.2	-1.7	10.7	4.7	3
Succulent Karoo	31	2.2	-0.7	4.3	1.8	1.4

$\delta^{18}O$ of Evaporation Insensitive ungulate species from all biomes

Appendix 8c: Summary statistics for $\delta^{13}C_{collagen}$ for each group discussed in Results

Type	Feeder Type	N	Median	Minimum	Maximum	Mean	Std. Deviation
Carnivore	Carnivore	32	-17.4	-20.9	-10.6	-16.6	3.4
Primate	Omnivore	145	-20.2	-22	-10.9	-19.5	2.2
Ungulate		251	-18.4	-24.8	-6.9	-16.6	4.6
	Browser	102	-20.0	-24.8	-14.8	-19.9	1.8
	Grazer	117	-12.3	-22.4	-6.9	-12.9	3.9
	Mixed feeder	19	-19.4	-21.3	-15.3	-19	1.7
	Omnivore	13	-20.8	-22.8	-19	-20.9	1

$\delta^{13}C_{collagen}$ of all animal groups highlighting differences across biomes

BY FEEDER TYPE

Biome	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany Thicket	18	-19.3	-22.6	-15.1	-18.8	2
Forest	16	-21.9	-24.8	-19.6	-21.9	1.4
Fynbos	14	-21.1	-22.2	-19.3	-20.9	0.8
Nama Karoo	5	-18.6	-20.2	-17.3	-18.6	1.1
Savanna	17	-20.0	-21	-19	-20.1	0.6
Succulent Karoo	32	-19.5	-23.2	-14.8	-19.3	1.5

$\delta^{13}C_{collagen}$ of browsing ungulate species highlighting differences across biomes

Biome	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany Thicket	47	-10.5	-17.5	-6.9	-10.8	2.7
Forest	4	-10.7	-16.6	-9.7	-11.9	3.3
Fynbos	14	-20.2	-22.4	-13.3	-19.4	2.5
Nama Karoo	1	-8.9	-8.9	-8.9	-8.9	
Savanna	24	-11.8	-16.5	-8.1	-11.2	2.3
Succulent Karoo	27	-15.8	-19.4	-9.7	-15.1	2.8

$\delta^{13}C_{collagen}$ of grazing ungulate species highlighting differences across biomes

Biome	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany Thicket						
Forest						
Fynbos						
Nama Karoo	9	-19.9	-20.6	-15.6	-19.5	1.5
Savanna	4	-17.2	-17.8	-15.3	-16.9	1.1
Succulent Karoo	6	-19.3	-21.3	-18.1	-19.6	1.3

$\delta^{13}C_{collagen}$ of mixed feeding ungulate species highlighting differences across biomes

	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany thicket	0					
Forest	13	-20.8	-22.9	-19	-20.9	1
Fynbos	0					
Nama Karoo	0					
Savanna	0					
Succulent Karoo	0					

$\delta^{13}C_{collagen}$ of omnivorous ungulates highlighting differences across biomes

Appendix 8c: Summary statistics for $\delta^{13}C_{collagen}$ for each group discussed in Results

	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany thicket	2	-14.1	-14.8	-13.5	-14.1	0.9
Forest	6	-18.0	-20.9	-13.1	-17.5	3
Fynbos	14	-19.5	-20.8	-13.1	-19	2
Nama Karoo	1	-15.1	-15.1	-15.1	-15.1	
Savanna	8	-12.5	-15.3	-10.6	-12.4	1.6
Succulent Karoo	1	-17.4	-17.4	-17.4	-17.4	

$\delta^{13}C_{collagen}$ of carnivores highlighting differences across biomes

Biome	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany thicket	8	-11.7	-13.8	-10.9	-12	1
Forest	11	-20.8	-21.5	-19	-20.6	0.8
Fynbos	97	-20.5	-22	-13.3	-20	1.5
Nama Karoo						
Savanna						
Succulent Karoo	29	-19.6	-21.2	-18.3	-19.6	0.5

$\delta^{13}C_{collagen}$ of primates highlighting differences across biomes

By BIOME

FeederType	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	18	-19.3	-22.6	-15.1	-18.8	2
Grazer	47	-10.5	-17.5	-6.9	-10.8	2.7
Carnivore	2	-14.1	-14.8	-13.5	-14.1	0.9
Omnivore	8	-11.7	-13.8	-10.9	-12	1

$\delta^{13}C_{collagen}$ of all species from the Albany Thicket biome

	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	16	-21.9	-24.8	-19.6	-21.9	1.4
Grazer	4	-10.7	-16.6	-9.7	-11.9	3.3
Omnivore	24	-18.0	-22.8	-19	-20.8	0.9
Carnivore	6	-20.8	-20.9	-13.1	-17.5	3

$\delta^{13}C_{collagen}$ of all species from the Forest biome

FeederType	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	14	-21.1	-22.2	-19.3	-20.9	0.8
Grazer	14	-20.2	-22.4	-13.3	-19.4	2.5
Carnivore	14	-19.5	-20.8	-13.1	-19	2
Omnivore	97	-20.5	-22	-13.3	-20	1.5

$\delta^{13}C_{collagen}$ of all species from the Fynbos biome

Appendix 8c: Summary statistics for $\delta^{13}C_{collagen}$ for each group discussed in Results

FeederType	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	5	-18.6	-20.2	-17.3	-18.6	1.1
Grazer	1	-8.9	-8.9	-8.9	-8.9	
Mixed	9	-19.9	-20.6	-15.6	-19.5	1.5
Carnivore	1	-15.1	-15.1	-15.1	-15.1	

$\delta^{13}C_{collagen}$ of all species from the Nama Karoo biome

	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	17	-20.0	-21	-19	-20.1	0.6
Grazer	24	-11.8	-16.5	-8.1	-11.2	2.3
Mixed	4	-17.2	-17.8	-15.3	-16.9	1.1
Omnivore						
Carnivore	8	-12.5	-15.3	-10.6	-12.4	1.6

$\delta^{13}C_{collagen}$ of all species from the Savanna biome

FeederType	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	32	-19.5	-23.2	-14.8	-19.3	1.5
Grazer	27	-15.8	-19.4	-9.7	-15.1	2.8
Mixed	6	-19.3	-21.3	-18.1	-19.6	1.3
Carnivore	1	-17.4	-17.4	-17.4	-17.4	
Omnivore	29	-19.6	-21.2	-18.3	-19.6	0.5

$\delta^{13}C_{collagen}$ of all species from the Succulent Karoo biome

Appendix 8d: Summary statistics for $\delta^{15}N_{collagen}$ for each group discussed in Results

Type	Feeder Type	N	Median	Minimum	Maximum	Mean	Std. Deviation
Carnivore	Carnivore	32	11.1	5.2	15.2	11.2	2.9
Primate	Omnivore	145	6.1	3.5	14.3	6.5	1.9
Ungulate		251	10.5	1.8	17.2	9.9	2.7
Browser	Browser	102	10.1	1.8	17.2	9.1	3.5
Grazer	Grazer	117	10.8	4.7	15.4	10.7	1.7
Mixed	Mixed feeder	19	11.5	9.3	13	11.3	1
Omnivore	Omnivore	13	6.34	4.4	8.7	6.5	1.3

$\delta^{15}N_{collagen}$ ofall animal groups highlighting differences across biomes

Biome	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany Thicket	18	11.4	8.2	13.3	11.2	1.4
Forest	16	3.7	2.9	10.7	4.7	2.1
Fynbos	16	5.9	1.8	16.1	8.2	4.6
Nama Karoo	4	10.1	6.6	10.5	9.2	1.7
Savanna	17	10.3	9.3	12.6	10.5	1
Succulent Karoo	31	10.9	4	17.2	9.8	3.2

$\delta^{15}N_{collagen}$ of browsing ungulate species highlighting differences across biomes

Biome	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany Thicket	47	11.2	4.7	13.5	11.3	1.4
Forest	4	8.8	5	11.9	8.6	3.3
Fynbos	15	10.3	5.4	13.7	9.9	2.2
Nama Karoo	1	9.0	9	9	9	
Savanna	24	10.4	8.2	12.3	10.4	1.1
Succulent Karoo	27	10.5	8.4	15.4	10.7	1.4

$\delta^{15}N$ of grazing ungulate species highlighting differences across biomes

	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany thicket						
Forest						
Fynbos						
Nama Karoo	9	11.9	9.8	13	11.6	1.1
Savanna	4	10.4	9.3	11.8	10.5	1
Succulent Karoo	6	11.3	10.3	12.4	11.3	0.8

$\delta^{15}N$ of mixed feeding ungulate species highlighting differences across biomes

Appendix 8d: Summary statistics for $\delta^{15}N_{collagen}$ for each group discussed in Results

	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany thicket						
Forest	13	6.3	4.4	8.7	6.5	1.3
Fynbos						
Nama Karoo						
Savanna						
Succulent Karoo						

$\delta^{15}N$ of omnivorous ungulates from all biomes (only collected in Forest biome)

	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany Thicket	2	15.0	14.9	15.2	15	0.2
Forest	6	8.2	6.6	10.8	8.3	1.5
Fynbos	14	10.6	5.2	14.7	10.1	2.4
Nama Karoo	1	10.8	10.8	10.8	10.8	
Savanna	8	14.2	12.7	15.1	14	0.8
Succulent Karoo	1	15.2	15.2	15.2	15.2	

$\delta^{15}N$ of carnivores highlighting differences across biomes

	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany Thicket	8	6.2	5.6	6.5	6.2	0.3
Forest	11	5.3	3.8	7.3	5.5	1.2
Fynbos	78	5.8	3.5	11	6.4	2.1
Nama Karoo						
Savanna						
Succulent Karoo	49	7.2	5.3	14.3	7	1.6

$\delta^{15}N$ of primates highlighting differences across biomes

By BIOME

	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	19	11.4	8.2	13.3	11.2	1.4
Carnivore	2	15.0	14.9	15.2	15	0.2
Grazer	41	11.2	4.7	13.5	11.3	1.5
Omnivore	15	6.2	5.6	12.7	8.3	2.6

$\delta^{15}N$ of all species from the Albany Thicket biome

	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	16	3.7	2.9	10.7	4.7	2.1
Carnivore	7	8.2	6.6	10.8	8.5	1.4
Grazer	4	8.8	5	11.9	8.6	3.3
Omnivore	45	5.9	3.8	8.7	5.7	1.1

$\delta^{15}N$ of all species from the Forest biome

Appendix 8d: Summary statistics for $\delta^{15}N_{collagen}$ for each group discussed in Results

FeederType	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	16	5.9	1.8	16.1	8.2	4.6
Carnivore	14	10.6	5.2	14.7	10.1	2.4
Grazer	18	10.3	5.4	13.7	9.2	2.5
Omnivore	97	5.8	3.5	11	6.4	1.9

δ^{15}N of all species from the Fynbos biome

	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	4	10.1	6.6	10.5	8.7	1.7
Carnivore	1	10.8	10.8	10.8	10.8	
Grazer	1	9.0	9	9	9	
Omnivore						
Mixed	9	11.9	9.8	13	11.6	1.1

δ^{15}N of all species from the Nama Karoo biome

	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	17	10.3	9.3	12.6	10.5	1
Carnivore	8	14.2	12.7	15.1	14	0.8
Grazer	24	10.4	8.2	12.3	10.4	1.1
Omnivore						
Mixed	4	10.4	9.3	11.8	10.5	1

δ^{15}N of all species from the Savanna biome

FeederType	N	Median	Minimum	Maximum	Mean	Std. Deviation
Browser	31	10.9	4	17.2	9.8	3.2
Carnivore	1	15.2	15.2	15.2	15.2	
Grazer	28	10.5	8.4	15.4	10.7	1.4
Mixed	6	11.3	10.3	12.4	11.3	0.8
Omnivore	29	7.2	6.1	14.3	7.6	1.7

δ^{15}N of all species from the Succulent Karoo biome

BY ES/EI

Biome	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany Thicket	31	10.8	8.7	15.2	11.2	1.4
Forest	10	3.9	2.9	10.8	6.2	2.7
Fynbos	26	9.8	1.8	16.1	9.5	3.4
Nama Karoo	14	11.5	9	13	11	1.2
Savanna	38	10.3	8.9	15.1	11.1	1.7
Succulent Karoo	63	10.8	4	17.2	10.4	2.6

δ^{15}N of Water Independent ungulate species from all biomes

Appendix 8d: Summary statistics for $\delta^{15}N_{collagen}$ for each group discussed in Results

Biome	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany Thicket	34	12.1	4.7	13.5	10.5	2.6
Forest	23	6.0	3.1	11.9	6	2
Fynbos	2	6.6	3.5	11	6.4	1.9
Nama Karoo	1	6.6	6.6	6.6	6.6	
Savanna	7	10.1	8.2	12.4	10.3	1.4
Succulent Karoo	2	9.5	6.1	14.3	7.7	1.7

$\delta^{15}N$ of Water Dependent ungulate species from all biomes

Biome	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany Thicket	18	11.4	8.2	15.2	11.5	1.8
Forest	16	3.7	2.9	10.8	5.7	2.5
Fynbos	14	5.9	1.8	16.1	9.1	3.8
Nama Karoo	13	11.8	9.6	13	11.2	1.1
Savanna	21	10.3	9.3	15.1	11.5	1.9
Succulent Karoo	38	11.0	4	17.2	10.2	3.1

$\delta^{15}N$ of Evaporation sensitive ungulate species from all biomes

Biome	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany Thicket	47	11.2	4.7	13.51	11.3	2.3
Forest	17	6.6	3.82	11.85	7	1.9
Fynbos	14	10.3	3.49	13.66	9.9	2.3
Nama Karoo	2	7.8	6.62	8.97	7.8	1.7
Savanna	24	10.4	8.2	12.33	10.4	1.1
Succulent Karoo	27	10.5	6.1	15.37	10.7	2.2

$\delta^{15}N$ of Evaporation Insensitive ungulate species from all biomes

By Digestive physiology

	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany thicket	7	10.3	9.1	12.7	10.9	1.4
Forest	13	6.3	4.4	8.7	6.5	1.3
Fynbos						
Nama Karoo	1	6.6	6.6	6.6	6.6	
Savanna						
Succulent Karoo	2	9.5	9.4	9.7	9.5	0.2

$\delta^{15}N$ of non-ruminant (hindgut) ungulate species from all biomes

Biome	N	Median	Minimum	Maximum	Mean	Std. Deviation
Albany Thicket	58	11.4	4.7	13.5	11.3	1.4
Forest	20	4.7	2.9	11.9	5.5	2.8
Fynbos	30	9.3	1.8	16.1	9	3.7
Nama Karoo	13	11.5	9	13	11	1.3
Savanna	45	10.3	8.2	12.6	10.4	1.1
Succulent Karoo	62	10.8	4	17.2	10.4	2.5

$\delta^{15}N$ of ruminant ungulate species from all biomes

APPENDIX 9

Outcome of regression models by individual meteorological factors

Appendix 9a: $\delta^{13}C_{enamel}$ for Ungulates **Carbon enamel**

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	-12.934	1.278	-10.121	.000	-15.449	-10.419
[Size=Extra large]	3.289	1.281	2.568	.011	.768	5.810
[Size=Large]	1.615	.527	3.065	.002	.578	2.652
[Size=Medium]	-.716	.773	-.926	.355	-2.237	.806
[Size=Small]	0[a]					
[FeederType=Browser]	-.317	1.054	-.300	.764	-2.392	1.758
[FeederType=Grazer]	8.173	1.052	7.766	.000	6.101	10.244
[FeederType=Mixed]	2.580	1.108	2.329	.021	.399	4.761
[FeederType=Omnivore]	0[a]					
MAP	-.001	.001	-1.089	.277	-.003	.001

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	-27.712	3.632	-7.630	.000	-34.861	-20.563
[Size=Extra large]	2.524	1.264	1.996	.047	.035	5.013
[Size=Large]	.538	.583	.923	.357	-.609	1.686
[Size=Medium]	-1.531	.746	-2.053	.041	-2.999	-.063
[Size=Small]	0[a]					
[FeederType=Browser]	-.421	.976	-.431	.667	-2.342	1.501
[FeederType=Grazer]	8.388	.960	8.742	.000	6.499	10.276
[FeederType=Mixed]	3.389	.844	4.018	.000	1.729	5.050
[FeederType=Omnivore]	0[a]					
MAT	.876	.218	4.014	.000	.446	1.306

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	-14.013	4.264	-3.286	.001	-22.409	-5.617
[Size=Extra large]	3.448	1.500	2.298	.022	.494	6.402
[Size=Large]	1.393	.588	2.368	.019	.235	2.551
[Size=Medium]	-.265	.857	-.309	.757	-1.952	1.422
[Size=Small]	0[a]					
[FeederType=Browser]	-4.031	2.924	-1.379	.169	-9.788	1.726
[FeederType=Grazer]	4.328	2.903	1.491	.137	-1.389	10.044
[FeederType=Mixed]	-1.885	2.883	-.654	.514	-7.561	3.791
[FeederType=Omnivore]	0[a]					
MASMS	.059	.044	1.323	.187	-.029	.146

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	-14.851	1.380	-10.764	.000	-17.567	-12.135
[Size=Extra large]	3.141	1.289	2.436	.015	.603	5.678
[Size=Large]	1.508	.538	2.803	.005	.449	2.567
[Size=Medium]	-.806	.754	-1.068	.286	-2.291	.679
[Size=Small]	0[a]					
[FeederType=Browser]	-.161	1.009	-.160	.873	-2.148	1.825
[FeederType=Grazer]	8.388	.994	8.435	.000	6.430	10.345
[FeederType=Mixed]	2.839	.950	2.988	.003	.969	4.709
[FeederType=Omnivore]	0[a]					
MAPE	.001	.000	1.257	.210	.000	.002

APPENDIX 9

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	-13.780	1.520	-9.064	.000	-16.773	-10.788
[Size=Extra large]	3.358	1.301	2.581	.010	.797	5.920
[Size=Large]	1.661	.542	3.063	.002	.594	2.729
[Size=Medium]	-.926	.752	-1.231	.219	-2.406	.554
[Size=Small]	0[a]					
[FeederType=Browser]	.068	.996	.068	.946	-1.892	2.028
[FeederType=Grazer]	8.582	.985	8.713	.000	6.643	10.521
[FeederType=Mixed]	3.344	.887	3.769	.000	1.597	5.090
[FeederType=Omnivore]	0[a]					
RH	.001	.015	.049	.961	-.030	.031

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	-14.627	1.033	-14.156	.000	-16.661	-12.593
[Size=Extra large]	1.387	1.306	1.063	.289	-1.182	3.957
[Size=Large]	.249	.590	.422	.674	-.913	1.411
[Size=Medium]	-2.328	.784	-2.970	.003	-3.871	-.785
[Size=Small]	0[a]					
[FeederType=Browser]	.337	.962	.351	.726	-1.555	2.230
[FeederType=Grazer]	9.397	.965	9.734	.000	7.497	11.297
[FeederType=Mixed]	5.201	.927	5.613	.000	3.377	7.025
[FeederType=Omnivore]	0[a]					
SAI	.012	.003	4.663	.000	.007	.017

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	-12.279	1.200	-10.236	.000	-14.640	-9.918
[Size=Extra large]	2.539	1.312	1.935	.054	-.043	5.121
[Size=Large]	.896	.607	1.475	.141	-.300	2.091
[Size=Medium]	-1.417	.770	-1.840	.067	-2.932	.099
[Size=Small]	0[a]					
[FeederType=Browser]	-.292	.996	-.293	.770	-2.253	1.669
[FeederType=Grazer]	8.374	.979	8.557	.000	6.448	10.300
[FeederType=Mixed]	3.032	.867	3.498	.001	1.326	4.739
[FeederType=Omnivore]	0[a]					
WCR	-.023	.009	-2.437	.015	-.041	-.004

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	-14.245	1.129	-12.616	.000	-16.467	-12.022
[Size=Extra large]	3.178	1.286	2.471	.014	.647	5.709
[Size=Large]	1.535	.534	2.876	.004	.484	2.586
[Size=Medium]	-.764	.759	-1.006	.315	-2.259	.731
[Size=Small]	0[a]					
[FeederType=Browser]	-.236	1.022	-.231	.818	-2.247	1.776
[FeederType=Grazer]	8.294	1.009	8.221	.000	6.308	10.280
[FeederType=Mixed]	2.706	1.000	2.706	.007	.737	4.675
[FeederType=Omnivore]	0[a]					
WD	.000	.000	1.250	.212	.000	.001

APPENDIX 9

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	Upper Bound
Intercept	-12.561	1.255	-10.008	.000	-15.031	-10.090
[Size=Extra large]	3.278	1.277	2.568	.011	.766	5.791
[Size=Large]	1.566	.527	2.973	.003	.529	2.603
[Size=Medium]	-.626	.768	-.816	.415	-2.137	.885
[Size=Small]	0[a]					
[FeederType=Browser]	-.603	1.067	-.565	.573	-2.704	1.498
[FeederType=Grazer]	7.873	1.067	7.382	.000	5.774	9.972
[FeederType=Mixed]	2.111	1.127	1.874	.062	-.107	4.329
[FeederType=Omnivore]	0[a]					
MI	-2.922	1.732	-1.687	.093	-6.332	.487

Best fit model for Ungulates

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	-16.696	1.573	-10.614	.000	-19.792	-13.600
[FeederType=Browser]	.407	.959	.425	.671	-1.480	2.295
[FeederType=Grazer]	9.480	.963	9.843	.000	7.584	11.376
[FeederType=Mixed]	5.787	.983	5.888	.000	3.853	7.722
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	1.519	1.303	1.166	.245	-1.046	4.084
[Size=Large]	.292	.589	.495	.621	-.868	1.451
[Size=Medium]	-2.599	.796	-3.263	.001	-4.167	-1.031
[Size=Small]	0[a]					
RH	.027	.016	1.740	.083	-.004	.059
SAI	.013	.003	4.993	.000	.008	.019

a. R Squared = .760 (Adjusted R Squared = .753)

Appendix 9b: : $\delta^{13}C_{enamel}$ for Carnivores

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	Upper Bound
Intercept	-8.430	.900	-9.371	.000	-10.265	-6.595
MAP	-.008	.002	-4.635	.000	-.011	-.004

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	-45.343	5.548	-8.173	.000	-56.658	-34.028
MAT	1.969	.328	6.004	.000	1.300	2.637

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	-37.557	3.629	-10.349	.000	-45.047	-30.067
MASMS	.338	.047	7.161	.000	.241	.435

APPENDIX 9

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	-21.715	1.903	-11.409	.000	-25.597	-17.833
MAPE	.004	.001	5.164	.000	.003	.006

Dependent Variable:

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	-0.579	2.184	-0.265	.793	-5.033	3.876
RH	-.171	.032	-5.368	.000	-.236	-.106

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	-13.505	.818	-16.516	.000	-15.172	-11.837
SAI	.012	.005	2.189	.036	.001	.023

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	-9.432	.770	-12.253	.000	-11.002	-7.862
WCR	-.062	.015	-4.232	.000	-.092	-.032

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	-17.150	1.048	-16.363	.000	-19.287	-15.012
WD	.003	.001	5.207	.000	.002	.004

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	-9.371	.779	-12.027	.000	-10.960	-7.782
MI	-10.994	2.588	-4.248	.000	-16.273	-5.716

Best fit model for Canivores

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	-1.129	2.820	-0.400	.692	-6.889	4.630
SAI	.002	.005	.316	.754	-.008	.012
RH	-.166	.037	-4.506	.000	-.241	-.090

a. R Squared = .483 (Adjusted R Squared = .449)

APPENDIX 9

Appendix 9c : $\delta^{13}C_{enamel}$ for Primates

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	-12.258	.504	-24.341	.000	-13.253	-11.262
MAP	-.004	.001	-3.722	.000	-.006	-.002

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	-26.465	4.075	-6.495	.000	-34.519	-18.411
MAT	.778	.254	3.062	.003	.276	1.280

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	-33.888	3.691	-9.181	.000	-41.189	-26.587
MASMS	.270	.050	5.429	.000	.172	.369

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	-19.824	1.545	-12.828	.000	-22.879	-16.770
MAPE	.003	.001	3.794	.000	.001	.004

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	-13.464	1.814	-7.421	.000	-17.050	-9.878
RH	-.007	.025	-0.298	.766	-.057	.042

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	-14.131	.251	-56.202	.000	-14.628	-13.634
SAI	.002	.002	0.798	.426	-.003	.007

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	-11.707	.486	-24.089	.000	-12.667	-10.746
WCR	-.044	.009	-5.074	.000	-.061	-.027

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	-16.694	.722	-23.126	.000	-18.121	-15.267
WD	.002	.000	3.857	.000	.001	.003

APPENDIX 9

Parameter	B	Std. Error	t	Sig.	Interval	
					Lower Bound	Upper Bound
Intercept	-12.499	.414	-30.169	.000	-13.317	-11.680
MI	-6.291	1.556	-4.044	.000	-9.366	-3.216

Best fit for primates

Parameter	B	Std. Error	t	Sig.	95% Confidence	
					Lower Bound	Upper Bound
Intercept	-13.263	1.830	-7.248	.000	-16.881	-9.646
SAI	.002	.002	.879	.381	-.003	.007
RH	-.012	.026	-.479	.633	-.063	.038

a. R Squared = .006 (Adjusted R Squared = -.008)

Appendix 9d: $\delta^{18}O_{enamel}$ for Ungulates **Oxygen**

Parameter	B	Std. Error	t	Sig.	95% Confidence	
					Lower Bound	Upper Bound
Intercept	7.476	1.230	6.080	.000	5.056	9.896
MAP	-.013	.001	-12.066	.000	-.015	-.011
[FeederType=Browser]	-2.052	1.014	-2.024	.044	-4.049	-.056
[FeederType=Grazer]	-3.831	1.013	-3.783	.000	-5.824	-1.838
[FeederType=Mixed]	2.743	1.066	2.573	.011	.644	4.842
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	-.487	1.232	-.395	.693	-2.912	1.939
[Size=Large]	1.824	.507	3.599	.000	.826	2.822
[Size=Medium]	-2.810	.744	-3.778	.000	-4.274	-1.346
[Size=Small]	0[a]					

Parameter	B	Std. Error	t	Sig.	Interval	
					Lower Bound	Upper Bound
Intercept	-25.773	4.129	-6.242	.000	-33.900	-17.646
[FeederType=Browser]	1.171	1.110	1.055	.292	-1.014	3.355
[FeederType=Grazer]	.191	1.091	.175	.861	-1.956	2.338
[FeederType=Mixed]	10.879	.959	11.343	.000	8.991	12.766
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	-1.320	1.437	-.918	.359	-4.149	1.509
[Size=Large]	.274	.663	.413	.680	-1.031	1.578
[Size=Medium]	-6.105	.848	-7.200	.000	-7.774	-4.436
[Size=Small]	0[a]					
MAT	1.554	.248	6.262	.000	1.065	2.042

APPENDIX 9

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	-26.524	4.043	-6.560	.000	-34.485	-18.562
[FeederType=Browser]	-2.529	2.772	-.912	.363	-7.988	2.930
[FeederType=Grazer]	-3.841	2.753	-1.395	.164	-9.261	1.580
[FeederType=Mixed]	3.380	2.733	1.236	.217	-2.003	8.762
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	-2.906	1.423	-2.043	.042	-5.707	-.105
[Size=Large]	-.149	.558	-.267	.790	-1.247	.949
[Size=Medium]	-5.061	.813	-6.228	.000	-6.660	-3.461
[Size=Small]	0[a]					
MASMS	.400	.042	9.498	.000	.317	.484

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	-12.037	1.283	-9.385	.000	-14.561	-9.512
[FeederType=Browser]	-.208	.938	-.222	.825	-2.055	1.639
[FeederType=Grazer]	-1.383	.924	-1.496	.136	-3.202	.436
[FeederType=Mixed]	5.904	.883	6.683	.000	4.165	7.642
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	-1.894	1.198	-1.580	.115	-4.253	.465
[Size=Large]	.809	.500	1.618	.107	-.175	1.794
[Size=Medium]	-3.866	.701	-5.513	.000	-5.247	-2.486
[Size=Small]	0[a]					
MAPE	.006	.000	13.305	.000	.005	.007

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	9.728	1.564	6.218	.000	6.649	12.807
[FeederType=Browser]	1.850	1.025	1.806	.072	-.167	3.867
[FeederType=Grazer]	.678	1.013	.669	.504	-1.317	2.673
[FeederType=Mixed]	8.938	.913	9.790	.000	7.141	10.735
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	-2.025	1.339	-1.512	.132	-4.661	.610
[Size=Large]	.987	.558	1.768	.078	-.112	2.085
[Size=Medium]	-4.572	.774	-5.908	.000	-6.095	-3.049
[Size=Small]	0[a]					
RH	-.151	.016	-9.478	.000	-.182	-.120

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	-1.009	1.264	-.798	.426	-3.497	1.480
[FeederType=Browser]	2.047	1.176	1.740	.083	-.268	4.363
[FeederType=Grazer]	.574	1.181	.486	.628	-1.751	2.898
[FeederType=Mixed]	10.866	1.134	9.585	.000	8.635	13.098
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	.051	1.597	.032	.974	-3.093	3.195
[Size=Large]	2.191	.722	3.032	.003	.769	3.613
[Size=Medium]	-5.091	.959	-5.309	.000	-6.979	-3.204
[Size=Small]	0[a]					
SAI	.001	.003	.173	.862	-.006	.007

APPENDIX 9

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	1.963	1.386	1.416	.158	-.765	4.691
[FeederType=Browser]	1.309	1.151	1.137	.256	-.957	3.575
[FeederType=Grazer]	.114	1.131	.101	.920	-2.112	2.339
[FeederType=Mixed]	10.169	1.002	10.152	.000	8.198	12.141
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	-1.498	1.516	-.988	.324	-4.481	1.486
[Size=Large]	.717	.702	1.021	.308	-.665	2.098
[Size=Medium]	-6.026	.890	-6.773	.000	-7.777	-4.274
[Size=Small]	0[a]					
WCR	-.046	.011	-4.271	.000	-.067	-.025

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	-6.187	1.038	-5.960	.000	-8.230	-4.144
[FeederType=Browser]	-1.008	.940	-1.073	.284	-2.858	.841
[FeederType=Grazer]	-2.366	.928	-2.550	.011	-4.192	-.540
[FeederType=Mixed]	4.454	.920	4.844	.000	2.644	6.264
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	-1.565	1.182	-1.324	.187	-3.892	.762
[Size=Large]	1.048	.491	2.135	.034	.082	2.014
[Size=Medium]	-3.417	.698	-4.894	.000	-4.792	-2.043
[Size=Small]	0[a]					
WD	.004	.000	13.684	.000	.004	.005

APPENDIX 9

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	Upper Bound
Intercept	7.301	1.194	6.118	.000	4.952	9.651
[FeederType=Browser]	-2.716	1.015	-2.676	.008	-4.714	-.718
[FeederType=Grazer]	-4.499	1.014	-4.436	.000	-6.495	-2.503
[FeederType=Mixed]	2.104	1.072	1.964	.051	-.005	4.213
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	-.351	1.214	-.289	.773	-2.740	2.039
[Size=Large]	1.623	.501	3.240	.001	.637	2.608
[Size=Medium]	-2.916	.730	-3.995	.000	-4.352	-1.479
[Size=Small]	0[a]					
MI	-20.732	1.647	-12.585	.000	-23.974	-17.489

Best fit model for ungulates

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	Upper Bound
Intercept	-16.711	1.812	-9.220	.000	-20.279	-13.144
[FeederType=Browser]	-.051	.920	-.055	.956	-1.863	1.761
[FeederType=Grazer]	-1.414	.906	-1.561	.120	-3.197	.369
[FeederType=Mixed]	5.437	.875	6.210	.000	3.714	7.160
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	-.932	1.205	-.773	.440	-3.303	1.440
[Size=Large]	1.806	.564	3.204	.002	.697	2.916
[Size=Medium]	-2.798	.749	-3.734	.000	-4.273	-1.323
[Size=Small]	0[a]					
MAPE	.007	.001	12.971	.000	.006	.008
WCR	.038	.011	3.580	.000	.017	.059

a. R Squared = .654 (Adjusted R Squared = .644)

Appendix 9e: $\delta^{18}O_{enamel}$ for Carnivores

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	Upper Bound
Intercept	.437	.932	.469	.643	-1.464	2.338
MAP	-.007	.002	-4.220	.000	-.011	-.004

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	-3.991	8.151	-.490	.628	-20.615	12.632
MAT	.057	.482	0.118	.907	-.926	1.039

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	-1.752	4.191	-.418	.680	-10.402	6.898
MASMS	-.002	.055	-0.036	.972	-.114	.111

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	-8.770	2.370	-3.700	.001	-13.604	-3.936
MAPE	.003	.001	2.476	.019	.000	.005

APPENDIX 9

Parameter	B	Std. Error	t	Sig.	Interval	
					Lower Bound	Upper Bound
Intercept	-.483	2.996	-.161	.873	-6.593	5.627
RH	-.038	.044	-0.866	.393	-.127	.051

Parameter	B	Std. Error	t	Sig.	Interval	
					Lower Bound	Upper Bound
Intercept	-1.395	.792	-1.760	.088	-3.011	0.221
SAI	-.014	.005	-2.655	.012	-.025	-.003

Parameter	B	Std. Error	t	Sig.	Interval	
					Lower Bound	Upper Bound
Intercept	-3.785	.952	-3.976	.000	-5.727	-1.843
WCR	.017	.018	0.959	.345	-.020	.054

Parameter	B	Std. Error	t	Sig.	Interval	
					Lower Bound	Upper Bound
Intercept	-6.629	1.252	-5.294	.000	-9.182	-4.075
WD	.002	.001	3.108	.004	.001	.003

Parameter	B	Std. Error	t	Sig.	Interval	
					Lower Bound	Upper Bound
Intercept	-.207	.763	-.272	.788	-1.764	1.349
MI	-11.351	2.535	-4.478	.000	-16.520	-6.181

<u>Best fit model for carnivores</u>

Parameter	B	Std. Error	t	Sig.	95% Confidence	
					Lower Bound	Upper Bound
Intercept	-16.564	2.964	-5.588	.000	-22.617	-10.511
MAPE	.005	.001	4.457	.000	.003	.007
WCR	.063	.018	3.587	.001	.027	.099

a. R Squared = .416 (Adjusted R Squared = .377)

APPENDIX 9

Appendix 9f: $\delta^{18}O_{enamel}$ for Primates

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	Upper Bound
Intercept	2.337	.474	4.932	.000	1.400	3.273
MAP	-.007	.001	-7.498	.000	-.009	-.005

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	-6.424	4.433	-1.449	.149	-15.185	2.338
MAT	.340	.276	1.232	.220	-.206	.887

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	-19.612	3.882	-5.052	.000	-27.291	-11.934
MASMS	.254	.052	4.855	.000	.151	.358

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	-10.393	1.524	-6.817	.000	-13.406	-7.380
MAPE	.005	.001	6.226	.000	.003	.006

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	6.853	1.808	3.790	.000	3.279	10.426
RH	-.108	.025	-4.351	.000	-.158	-.059

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	0.099	.228	0.432	.666	-0.353	0.550
SAI	-.016	.002	-7.267	.000	-.020	-.011

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	-0.676	.558	-1.211	.228	-1.780	0.428
WCR	-.006	.010	-0.564	.574	-.025	.014

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	-5.640	.695	-8.112	.000	-7.015	-4.266
WD	.003	.000	6.946	.000	.002	.004

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	1.601	.397	4.032	.000	0.816	2.386
MI	-10.754	1.491	-7.214	.000	-13.701	-7.808

APPENDIX 9

Best fit model for primates

Parameter	B	Std. Error	t	Sig.	95% Confidence	
					Lower Bound	Upper Bound
Intercept	-11.523	1.786	-6.450	.000	-15.054	-7.992
MAPE	.005	.001	6.320	.000	.003	.006
WCR	.011	.009	1.208	.229	-.007	.029

a. R Squared = .220 (Adjusted R Squared = .209)

Appendix 9g: $\delta^{13}C_{collagen}$ for Ungulates

Carbon Collagen

Parameter	B	Std. Error	t	Sig.	95% Confidence	
					Lower Bound	Upper Bound
Intercept	-19.780	1.385	-14.281	.000	-22.508	-17.052
[FeederType=Browser]	.206	1.165	.177	.860	-2.089	2.501
[FeederType=Grazer]	6.865	1.172	5.859	.000	4.557	9.173
[FeederType=Mixed]	1.348	1.344	1.004	.317	-1.298	3.995
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	1.964	1.365	1.439	.151	-.724	4.652
[Size=Large]	.323	.631	.512	.609	-.919	1.566
[Size=Medium]	-.485	.879	-.552	.582	-2.217	1.247
[Size=Small]	0[a]					
MAP	-.001	.001	-.673	.501	-.003	.001

Parameter	B	Std. Error	t	Sig.	Interval	
					Lower Bound	Upper Bound
Intercept	-41.451	4.157	-9.972	.000	-49.638	-33.263
[FeederType=Browser]	-.220	1.070	-.206	.837	-2.327	1.887
[FeederType=Grazer]	7.040	1.057	6.658	.000	4.957	9.122
[FeederType=Mixed]	1.790	1.062	1.686	.093	-0.301	3.881
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	0.642	1.297	0.495	.621	-1.913	3.198
[Size=Large]	-1.232	.666	-1.851	.065	-2.544	0.079
[Size=Medium]	-1.499	.808	-1.856	.065	-3.090	0.092
[Size=Small]	0[a]					
MAT	1.319	.249	5.300	.000	.829	1.809

Parameter	B	Std. Error	t	Sig.	Interval	
					Lower Bound	Upper Bound
Intercept	-31.918	4.676	-6.826	.000	-41.136	-22.700
[FeederType=Browser]	.683	1.209	.565	.573	-1.701	3.066
[FeederType=Grazer]	7.279	1.166	6.244	.000	4.981	9.577
[FeederType=Mixed]	0[a]					
[Size=Extra large]	1.744	1.911	.912	.363	-2.024	5.512
[Size=Large]	-.178	.719	-.248	.804	-1.595	1.239
[Size=Medium]	.518	1.023	.506	.613	-1.499	2.534
[Size=Small]	0[a]					
MASMS	.149	.054	2.751	.006	.042	.256

APPENDIX 9

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	-21.337	1.605	-13.295	.000	-24.498	-18.176
[FeederType=Browser]	.235	1.135	.207	.836	-2.000	2.470
[FeederType=Grazer]	6.956	1.124	6.189	.000	4.742	9.169
[FeederType=Mixed]	1.356	1.220	1.111	.268	-1.047	3.759
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	1.818	1.347	1.350	.178	-.835	4.471
[Size=Large]	.232	.636	.365	.716	-1.021	1.485
[Size=Medium]	-.513	.849	-.604	.546	-2.185	1.159
[Size=Small]	0[a]					
MAPE	.001	.001	1.010	.313	-.001	.002

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	-18.843	1.763	-10.687	.000	-22.316	-15.370
[FeederType=Browser]	.388	1.120	.347	.729	-1.818	2.595
[FeederType=Grazer]	7.147	1.114	6.415	.000	4.953	9.342
[FeederType=Mixed]	1.571	1.147	1.370	.172	-.688	3.830
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	1.660	1.355	1.225	.222	-1.009	4.328
[Size=Large]	.200	.639	.313	.755	-1.059	1.459
[Size=Medium]	-.591	.838	-.706	.481	-2.241	1.059
[Size=Small]	0[a]					
RH	-.020	.019	-1.085	.279	-.057	.016

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	-21.838	1.105	-19.761	.000	-24.015	-19.662
[FeederType=Browser]	.874	1.019	.857	.392	-1.134	2.881
[FeederType=Grazer]	8.706	1.035	8.409	.000	6.667	10.745
[FeederType=Mixed]	4.912	1.099	4.469	.000	2.747	7.077
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	-1.833	1.322	-1.387	.167	-4.437	.771
[Size=Large]	-1.906	.649	-2.939	.004	-3.184	-.629
[Size=Medium]	-3.197	.834	-3.835	.000	-4.839	-1.555
[Size=Small]	0[a]					
SAI	.020	.003	7.294	.000	.014	.025

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	-16.229	1.175	-13.815	.000	-18.543	-13.915
[FeederType=Browser]	-.461	1.004	-.459	.647	-2.438	1.517
[FeederType=Grazer]	6.972	.993	7.022	.000	5.016	8.928
[FeederType=Mixed]	.973	1.003	.970	.333	-1.002	2.947
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	-.088	1.223	-.072	.943	-2.498	2.322
[Size=Large]	-1.617	.611	-2.646	.009	-2.820	-.413
[Size=Medium]	-1.838	.758	-2.425	.016	-3.331	-.345
[Size=Small]	0[a]					
WCR	-.071	.009	-8.048	.000	-.089	-.054

APPENDIX 9

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	-20.720	1.295	-15.999	.000	-23.271	-18.169
[FeederType=Browser]	.201	1.145	.176	.860	-2.053	2.456
[FeederType=Grazer]	6.896	1.137	6.066	.000	4.657	9.136
[FeederType=Mixed]	1.299	1.265	1.027	.306	-1.193	3.792
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	1.887	1.349	1.399	.163	-.770	4.543
[Size=Large]	.266	.633	.419	.675	-.981	1.512
[Size=Medium]	-.483	.859	-.562	.574	-2.175	1.209
[Size=Small]	0[a]					
WD	.000	.000	.929	.354	.000	.001

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	-19.553	1.357	-14.411	.000	-22.226	-16.881
[FeederType=Browser]	.040	1.173	.034	.973	-2.271	2.351
[FeederType=Grazer]	6.680	1.182	5.654	.000	4.353	9.007
[FeederType=Mixed]	1.026	1.353	.759	.449	-1.638	3.691
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	2.064	1.365	1.512	.132	-.624	4.752
[Size=Large]	.309	.630	.491	.624	-.932	1.550
[Size=Medium]	-.393	.873	-.450	.653	-2.112	1.326
[Size=Small]	0[a]					
MI	-1.876	1.737	-1.080	.281	-5.297	1.545

a. This parameter is set to zero because it is redundant.

Best fit model for ungulates Carbon collagen

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	-12.286	2.095	-5.864	.000	-16.412	-8.159
[FeederType=Browser]	.348	.972	.358	.721	-1.566	2.261
[FeederType=Grazer]	8.192	.985	8.316	.000	6.252	10.133
[FeederType=Mixed]	4.035	1.142	3.535	.000	1.787	6.284
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	-1.746	1.239	-1.409	.160	-4.186	.695
[Size=Large]	-2.376	.613	-3.878	.000	-3.583	-1.169
[Size=Medium]	-3.585	.803	-4.463	.000	-5.168	-2.003
[Size=Small]	0[a]					
MAPE	-.002	.001	-3.613	.000	-.003	-.001
WCR	-.078	.013	-6.059	.000	-.104	-.053
SAI	.008	.003	2.505	.013	.002	.014

a. R Squared = .691 (Adjusted R Squared = .680)

APPENDIX 9

Appendix 9h: $\delta^{13}C_{collagen}$ for Carnivores

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	Upper Bound
Intercept	-13.340	1.109	-12.027	.000	-15.605	-11.075
MAP	-.007	.002	-3.334	.002	-.011	-.003

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	-54.348	5.679	-9.571	.000	-65.946	-42.751
MAT	2.235	.335	6.663	.000	1.550	2.920

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	-44.880	4.043	-11.102	.000	-53.223	-36.537
MASMS	.373	.053	7.084	.000	.264	.481

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	-26.637	2.242	-11.883	.000	-31.215	-22.059
MAPE	.005	.001	4.579	.000	.003	.007

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	-3.828	2.334	-1.640	.112	-8.595	0.940
RH	-.190	.034	-5.567	.000	-.260	-.120

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	-18.825	0.806	-23.356	.000	-20.471	-17.179
SAI	.020	.005	3.576	.001	.008	.031

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	-12.941	0.686	-18.875	.000	-14.341	-11.540
WCR	-.084	.013	-6.521	.000	-.111	-.058

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	-21.712	1.289	-16.843	.000	-24.345	-19.079
WD	.003	.001	4.276	.000	.002	.004

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	-14.210	0.946	-15.020	.000	-16.142	-12.278
MI	-9.936	3.244	-3.062	.005	-16.562	-3.310

APPENDIX 9

Best fit model for carnivores

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	-17.770	4.146	-4.286	.000	-26.262	-9.277
MAPE	.002	.001	1.704	.099	.000	.004
WCR	-.069	.029	-2.378	.024	-.129	-.010
SAI	-.001	.008	-.142	.888	-.017	.015

a. R Squared = .639 (Adjusted R Squared = .600)

Appendix 9i: $\delta^{13}C_{collagen}$ for Primates

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	-18.531	.497	-37.282	.000	-19.513	-17.548
MAP	-.002	.001	-2.183	.031	-.004	.000

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	-29.270	3.985	-7.346	.000	-37.147	-21.394
MAT	.607	.248	2.444	.016	.116	1.098

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	-34.385	3.735	-9.205	.000	-41.774	-26.996
MASMS	.202	.050	4.002	.000	.102	.302

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	-22.828	1.529	-14.934	.000	-25.850	-19.807
MAPE	.002	.001	2.167	.032	.000	.003

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	-20.573	1.741	-11.819	.000	-24.014	-17.133
RH	.014	.024	0.597	.551	-.033	.062

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	-19.759	.241	-82.129	.000	-20.235	-19.284
SAI	.003	.002	1.412	.160	-.001	.008

APPENDIX 9

Parameter	B	Std. Error	t	Sig.	Interval	
					Lower Bound	Upper Bound
Intercept	-17.589	.475	-37.022	.000	-18.528	-16.650
WCR	-.037	.008	-4.412	.000	-.054	-.021

Parameter	B	Std. Error	t	Sig.	Interval	
					Lower Bound	Upper Bound
Intercept	-21.070	.712	-29.589	.000	-22.477	-19.662
WD	.001	.000	2.222	.028	.000	.002

Parameter	B	Std. Error	t	Sig.	Interval	
					Lower Bound	Upper Bound
Intercept	-18.611	.410	-45.366	.000	-19.422	-17.800
MI	-3.871	1.534	-2.523	.013	-6.904	-.839

Best fit model for primates

Parameter	B	Std. Error	t	Sig.	95% Confidence	
					Lower Bound	Upper Bound
Intercept	-19.124	3.060	-6.250	.000	-25.172	-13.075
MAPE	.001	.001	.640	.523	-.002	.003
WCR	-.036	.014	-2.600	.010	-.063	-.009
SAI	.000	.004	-.093	.926	-.008	.007

a. R Squared = .127 (Adjusted R Squared = .108)

Appendix 9j: $\delta^{15}N_{collagen}$ for Ungulates

Nitrogen

Parameter	B	Std. Error	t	Sig.	95% Confidence	
					Lower Bound	Upper Bound
Intercept	10.739	1.026	10.467	.000	8.718	12.760
[FeederType=Browser]	-.228	.863	-.264	.792	-1.928	1.472
[FeederType=Grazer]	.581	.868	.669	.504	-1.129	2.290
[FeederType=Mixed]	1.659	.995	1.666	.097	-.302	3.619
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	-.232	1.011	-.229	.819	-2.223	1.759
[Size=Large]	1.117	.467	2.391	.018	.197	2.038
[Size=Medium]	-.099	.651	-.152	.880	-1.382	1.184
[Size=Small]	0[a]					
MAP	-.005	.001	-5.709	.000	-.006	-.003

Parameter	B	Std. Error	t	Sig.	95% Confidence	
					Lower Bound	Upper Bound
Intercept	2.802	3.442	.814	.416	-3.977	9.581
[FeederType=Browser]	.961	.886	1.085	.279	-.784	2.705
[FeederType=Grazer]	2.085	.875	2.381	.018	.360	3.809
[FeederType=Mixed]	4.788	.879	5.447	.000	3.056	6.519
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	-1.398	1.074	-1.301	.194	-3.514	.718
[Size=Large]	.728	.551	1.321	.188	-.357	1.814
[Size=Medium]	-1.452	.669	-2.171	.031	-2.769	-.135
[Size=Small]	0[a]					
MAT	.309	.206	1.501	.135	-.097	.715

APPENDIX 9

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	9.310	3.249	2.865	.005	2.905	15.715
[FeederType=Browser]	-1.560	.840	-1.856	.065	-3.216	.096
[FeederType=Grazer]	-1.403	.810	-1.732	.085	-3.000	.194
[FeederType=Mixed]	0[a]					
[Size=Extra large]	-.608	1.328	-.458	.648	-3.226	2.010
[Size=Large]	1.260	.500	2.522	.012	.275	2.245
[Size=Medium]	.243	.711	.341	.733	-1.159	1.644
[Size=Small]	0[a]					
MASMS	.021	.038	.567	.572	-.053	.096

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	5.472	1.248	4.386	.000	3.015	7.930
[FeederType=Browser]	.721	.882	.817	.415	-1.017	2.458
[FeederType=Grazer]	1.780	.874	2.037	.043	.059	3.501
[FeederType=Mixed]	3.756	.949	3.960	.000	1.888	5.625
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	-1.131	1.047	-1.080	.281	-3.193	.932
[Size=Large]	.907	.494	1.835	.068	-.067	1.881
[Size=Medium]	-.926	.660	-1.402	.162	-2.226	.374
[Size=Small]	0[a]					
MAPE	.001	.000	2.756	.006	.000	.002

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	8.513	1.391	6.121	.000	5.774	11.253
[FeederType=Browser]	1.094	.883	1.239	.217	-.646	2.835
[FeederType=Grazer]	2.122	.879	2.414	.017	.390	3.853
[FeederType=Mixed]	4.655	.905	5.145	.000	2.873	6.437
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	-1.207	1.069	-1.129	.260	-3.312	.898
[Size=Large]	1.030	.504	2.041	.042	.036	2.023
[Size=Medium]	-1.216	.661	-1.840	.067	-2.517	.086
[Size=Small]	0[a]					
RH	-.011	.015	-.723	.470	-.039	.018

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	8.044	.956	8.410	.000	6.160	9.928
[FeederType=Browser]	1.033	.882	1.171	.243	-.705	2.770
[FeederType=Grazer]	1.827	.896	2.039	.043	.062	3.592
[FeederType=Mixed]	4.277	.951	4.496	.000	2.404	6.151
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	-.496	1.144	-.434	.665	-2.749	1.757
[Size=Large]	1.473	.561	2.624	.009	.367	2.578
[Size=Medium]	-.825	.721	-1.143	.254	-2.246	.596
[Size=Small]	0[a]					
SAI	-.003	.002	-1.441	.151	-.008	.001

APPENDIX 9

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	8.735	1.031	8.476	.000	6.705	10.765
[FeederType=Browser]	.900	.881	1.022	.308	-.835	2.635
[FeederType=Grazer]	2.068	.871	2.374	.018	.353	3.783
[FeederType=Mixed]	4.592	.879	5.221	.000	2.859	6.324
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	-1.578	1.073	-1.471	.143	-3.692	.536
[Size=Large]	.629	.536	1.174	.242	-.427	1.684
[Size=Medium]	-1.537	.665	-2.311	.022	-2.846	-.227
[Size=Small]	0[a]					
WCR	-.017	.008	-2.196	.029	-.032	-.002

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	6.298	.993	6.343	.000	4.342	8.254
[FeederType=Browser]	.425	.877	.484	.629	-1.303	2.153
[FeederType=Grazer]	1.438	.872	1.649	.100	-.279	3.155
[FeederType=Mixed]	3.069	.970	3.163	.002	1.158	4.980
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	-.920	1.034	-.889	.375	-2.957	1.117
[Size=Large]	.923	.485	1.902	.058	-.033	1.879
[Size=Medium]	-.669	.658	-1.017	.310	-1.966	.627
[Size=Small]	0[a]					
WD	.001	.000	3.821	.000	.001	.002

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	10.704	.997	10.738	.000	8.741	12.668
[FeederType=Browser]	-.478	.862	-.555	.580	-2.176	1.220
[FeederType=Grazer]	.311	.868	.358	.721	-1.399	2.021
[FeederType=Mixed]	1.352	.994	1.360	.175	-.605	3.309
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	-.108	1.003	-.108	.914	-2.083	1.867
[Size=Large]	1.051	.463	2.270	.024	.139	1.962
[Size=Medium]	-.097	.641	-.151	.880	-1.360	1.166
[Size=Small]	0[a]					
MI	-7.869	1.276	-6.167	.000	-10.383	-5.356

Best fit model for ungulates

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	95% Confidence Upper Bound
Intercept	6.326	1.678	3.771	.000	3.021	9.630
[FeederType=Browser]	.708	.883	.801	.424	-1.032	2.447
[FeederType=Grazer]	1.829	.877	2.085	.038	.101	3.556
[FeederType=Mixed]	3.871	.961	4.027	.000	1.977	5.764
[FeederType=Omnivore]	0[a]					
[Size=Extra large]	-1.322	1.078	-1.227	.221	-3.444	.801
[Size=Large]	.748	.537	1.391	.165	-.311	1.806
[Size=Medium]	-1.108	.703	-1.577	.116	-2.492	.276
[Size=Small]	0[a]					
MAPE	.001	.001	1.815	.071	-8E-05	.002
WCR	-.007	.009	-.762	.447	-.026	.011

a. R Squared = .262 (Adjusted R Squared = .238)

APPENDIX 9

Appendix 9k: $\delta^{15}N_{collagen}$ for Carnivores

Nitrogen

Parameter	B	Std. Error	t	Sig.	95% Confidence Lower Bound	Upper Bound
Intercept	15.563	.664	23.422	.000	14.206	16.921
MAP	-.009	.001	-7.387	.000	-.012	-.007

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	-15.441	5.933	-2.603	.014	-27.557	-3.325
MAT	1.580	.350	4.507	.000	.864	2.295

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	-8.692	3.688	-2.357	.027	-16.304	-1.080
MASMS	.269	.048	5.613	.000	.170	.368

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	1.722	1.774	0.971	.339	-1.901	5.344
MAPE	.004	.001	5.485	.000	.003	.006

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	20.069	2.342	8.569	.000	15.286	24.852
RH	-.131	.034	-3.837	.001	-.201	-.061

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	10.589	.813	13.028	.000	8.929	12.249
SAI	.006	.006	1.030	.311	-.006	.017

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	13.015	.825	15.768	.000	11.329	14.701
WCR	-.041	.016	-2.634	.013	-.073	-.009

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	5.811	.913	6.365	.000	3.946	7.675
WD	.003	.000	6.407	.000	.002	.004

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Upper Bound
Intercept	14.541	.576	25.234	.000	13.365	15.718
MI	-13.741	1.976	-6.953	.000	-17.777	-9.705

APPENDIX 9

Best fit model for carnivores

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	1.903	2.687	0.708	.485	-3.593	7.399
MAPE	.004	.001	4.265	.000	.002	.006
WCR	-.001	.016	-.091	.928	-.033	.030

a. R Squared = .501 (Adjusted R Squared = .466)

Appendix 9I: $\delta^{15}N_{collagen}$ for Primates

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	8.341	.391	21.343	.000	7.568	9.113
MAP	-.004	.001	-4.955	.000	-.005	-.002

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	15.254	3.326	4.586	.000	8.680	21.829
MAT	-.544	.207	-2.623	.010	-.953	-.134

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	-7.829	3.017	-2.595	.011	-13.796	-1.861
MASMS	.195	.041	4.796	.000	.115	.276

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	-1.417	1.115	-1.271	.206	-3.621	0.786
MAPE	.004	.001	7.188	.000	.003	.005

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	13.722	1.328	10.331	.000	11.096	16.347
RH	-.099	.018	-5.439	.000	-.136	-.063

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	7.004	.194	36.166	.000	6.621	7.387
SAI	-.007	.002	-3.721	.000	-.010	-.003

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	7.054	.421	16.737	.000	6.221	7.887
WCR	-.010	.008	-1.312	.192	-.025	.005

Parameter	B	Std. Error	t	Sig.	Interval Lower Bound	Interval Upper Bound
Intercept	3.253	.536	6.074	.000	2.195	4.312
WD	.002	.000	6.344	.000	.001	.003

APPENDIX 9

Parameter	B	Std. Error	t	Sig.	Interval	
					Lower Bound	Upper Bound
Intercept	8.052	.321	25.047	.000	7.416	8.687
MI	-6.306	1.202	-5.245	.000	-8.682	-3.929

Best fit model for primates

Parameter	B	Std. Error	t	Sig.	95% Confidence	
					Lower Bound	Upper Bound
Intercept	-1.760	1.306	-1.348	.180	-4.343	.822
MAPE	.004	.001	7.025	.000	.003	.005
WCR	.003	.007	.508	.613	-.010	.017

a. R Squared = .267 (Adjusted R Squared = .256)